ANNALS
OF THE
ENTOMOLOGICAL SOCIETY
OF AMERICA

Published by the
ENTOMOLOGICAL SOCIETY OF AMERICA
Formed in 1953 by Consolidation of the
American Association of Economic Entomologists
(1889-1952)
and the former
Entomological Society of America
(1906–1952)

Volume 49 **January, 1956** Number 1

ANNALS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA

Published by the
ENTOMOLOGICAL SOCIETY OF AMERICA
1530 P Street, N. W.
Washington 5, D. C.

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THE THOMAS SAY FOUNDATION. Five volumes have been published. Send inquiries and orders to Executive Secretary, Entomological Society of America, 1530 P Street, Washington 5, D. C.

Entered as second class matter April 11, 1908, at the Post Office at Columbus, Ohio, under the act of Congress of March 3, 1879. Subject to rate of postage provided for in Paragraph 4, Section 538, P. L. & R., authorized September 16, 1940.

Printed by The Spahr & Glenn Company,
Columbus, Ohio, U. S. A.

Issued February 29, 1956.

Annals of
The Entomological Society of America

Volume 49 JANUARY, 1956 No. 1

A CONTRIBUTION TOWARD A MONOGRAPH OF THE SCATOPSIDAE (DIPTERA) PART III, THE GENUS RHEXOZA ENDERLEIN[1]

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INTRODUCTION

The genus *Rhexoza* was established by Enderlein (1936, p. 55). The description, as in *Rhegmoclemina* already considered, is contained solely in a key to the genera of central Europe. The type species, *R. zacheri*, was a new species which was not described except for a figure of the wing, a size measurement, and an indication that it came from rotten potatoes.

The generic characters used by Enderlein are as follows: wings present; a clear fold between M and Cu (median suture); no macrotrichia on posterior veins nor wing membrane; M_1 not reduced basally; antennae 9 to 10 segmented; Cu_2 strongly bent posteriorly only once at or before the middle; the curvature of Cu_2 is more or less weak so that a prolongation of the end piece of Cu_2 basally would intersect M far basad of the M fork stem origin; the costal margin from Cu_1 to Cu_2 is smaller or no longer than that from M_2 to Cu_1; no crossvein stump present on M_1; one to several of the pale veins are completely reduced apically; the end piece of Cu_1, which is strongly bent posteriorly, is lacking.

This rather inadequate description, the fact that the type species is essentially undescribed and the fact that four unnamed species are also included in the genus is unfortunate. However, through the courtesy of Dr. Fritz Peus I have what is apparently the type specimen of *R. zacheri* available to me; this is a female. Before obtaining this specimen from Germany I had already tentatively recognized a distinct genus which included *Rhegmoclema aterrima* Melander, *Scatopse similis* Beekey, two and possibly three hitherto undescribed North American species and a single undescribed species from Panama. On the basis of the female genitalia and other characters this group is clearly congeneric with *R. zacheri*.

In this paper the apparent holotype of the type species will be redescribed, and the genus will be further described on the basis of the type and the new world species available. It is impossible at present to decide what central European species Enderlein had in mind for inclusion here. I have tentatively included in this genus four additional new world species which are rather distinctive. They are sufficiently so that they might be placed in two new genera. These are two species placed in the *Quatei* group and two species in the *Dampfi* group. The clearly typical species will be termed the *Zacheri* group. Until such time as the European fauna can be reworked on the basis of slide-mounted material, and until more is known of the group in the rest of the world, it seems best not to multiply generic names unnecessarily. In the formal description of *Rhexoza* that follows, the *Zacheri* group will be described first, with the *Quatei* and *Dampfi* groups immediately following until indications wherein they differ from the typical Zacheri form.

Rhexoza Enderlein

Rhexoza Enderlein, 1936. Die Tierwelt Mitteleuropas, 6, Lief. 2, Inseckten 3: 55. Type species: *Rhexoza zacheri* Enderlein, 1936.

GENERIC DESCRIPTION

Zacheri Group

The adults of the known species in this group range in size from 1.70–2.70 mm. in total length. The general coloration ranges from dark brown through grey-brown to black. The tarsi are usually yellowish or sordid white. Most of them are dull or feebly shining. The wings are clear in all species.

Head: The head is structurally similar to those of the three genera already described. The

[1]Paper No. 3283, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul 1, Minnesota.
Accepted for publication, Dec. 14, 1954.

antennae are always 10-segmented, no longer than the head height and dull black in color. The chaetotaxy of the head is as in the previously described genera except there are no setae on the upper margin of the clypeus.[2]

The mouthparts are like those of the Rhegmoclemini except that the maxillary palpi are larger, 0.10–0.15 mm long, decidedly slipper-shaped (fig. 2H) in profile and laterally compressed.

Thorax: The thorax is stoutly sclerotized, laterally compressed and very similar to that of *Rhegmoclema* in structure and chaetotaxy. A supraalar row of stout setae is present in all species. The anterior spiracular plate is triangular and bears the spiracle in the upper anterior angle or medially. A regular row of stout setae is present on the anepisternum before the wing base as in *Rhegmoclema*. There are 1 to 12 setae beneath the posterior spiracles.

The wings are as in the Rhegmoclemini with the following exceptions. There are no macrosetae on the posterior veins nor on the wing surface. Vein Cu_2 does not have two sharp bends along its course (figs. 1H, 2G, I). The second costal section is relatively longer than in *Rhegmoclemina*. The third section is from 2.5–4 times as long as the second. M^1 and M^2 are divergent throughout their length. M_2 is from 1.6–2.8 times as long as M.

The halteres are as in Rhegmoclemini except the pedicel bears several stout setae.

The tarsal segments are somewhat more slender than in the preceding genera, but they are otherwise similar.

Abdomen: There are seven obvious pregenital segments as in the Rhegmoclemini. The males have seven pairs of spiracles and the females eight. Segment 1 is the shortest. No reticulate pattern is present on tergum 1 of the male. Tergum 2 may sometimes be divided into two laterally located tergites and a larger medial posterior tergite. Terga and sterna bear scattered setae. The first three or four sterna are unsclerotized in both sexes. The abdominal membrane is longitudinally ribbed and folded and covered with scattered setae. Sternum 7 of the male is not shield-shaped. Tergum 8 of the male is usually present as a small median sclerite beneath tergum 7. There are no specialized setae on segment 6.

Male genitalia: The genitalia are rotated through 180° so the penis lies above tergum 9. In this group also the genitalia are small and largely withdrawn into segment 7. Tergum 9 is lobe-like and setaceous posteriorly. The penis is relatively short but stout and heavily sclerotized. Only a single pair of apically setaceous appendages is present. These are assumed to be the penis valves. The vesica is free and well developed.

Female genitalia: These structures offer excellent specific characters in this genus. Tergum 8 is either entire, divided into two plates or deeply incised. A pair of small spiracles is present in all species. Sternum 8 is also either deeply incised medially or divided into two plates. The cerci are rather larger than those of the Rhegmoclemini. A single heavily sclerotized spermatheca is present. This is spherical in all species except *R. panamensis* in which it is elongate.

[2]This character was overlooked heretofore. In all of the known Rhegmoclemini there are a few setae on the upper or posterior margin of the clypeus.

SUMMARY

1. Antennae 10-segmented.
2. Maxillary palpi slipper-shaped or somewhat reniform in side view, flattened laterally.
3. No setae on posterior wing veins.
4. Vein Cu_2 without two right-angled bends.
5. Setae present on pedicel of halter.
6. Male genitalia with a single pair of appendages.
7. Female terminalia with cerci only.
8. Tergum 8 of female terminalia bilobed or entire, sternum 8 deeply incised, entire or bilobed. Spiracles present on tergum 8.

Quatei Group

Among the specimens available to me are a number of very small forms from the southern part of the United States which constitute two distinct new species. These two species are closely related to each other but quite distinct from any heretofore described. From Duda's (1928, p. 283–285) description it seems probable that his *Scatopse auricularis* should be included here also. One species is known from Virginia, South Carolina and Texas, another from central and southern California, and, as noted above, a third has been described from Mexico. The species constituting this group are small (1.2-1.9 mm. long), dark grey-brown to black and feebly shining.

The following anatomical features serve to separate this group from the *Zacheri* group: tergum 7 of male is weakly sclerotized medially and rather reduced; tergum 8 present, partially retracted beneath 7; tergum 8 drawn out into two posteriorly directed, setaceous processes.

Male genitalia: Genitalia strongly compressed laterally. Tergum 9 (located ventrally) drawn out into a median, ventrally-directed, beak-like process. Penis small, slender and located dorsally at base of genitalia. A single pair of appendages (penis valves) present. Genital vesica and apodemes quite small, p.12 mm. long.

Female genitalia: Tergum 8 longitudinally divided and thus distinct from that of the *Zacheri* group and most other genera considered. Spiracles present on tergum 8. Sternum 8 reduced and

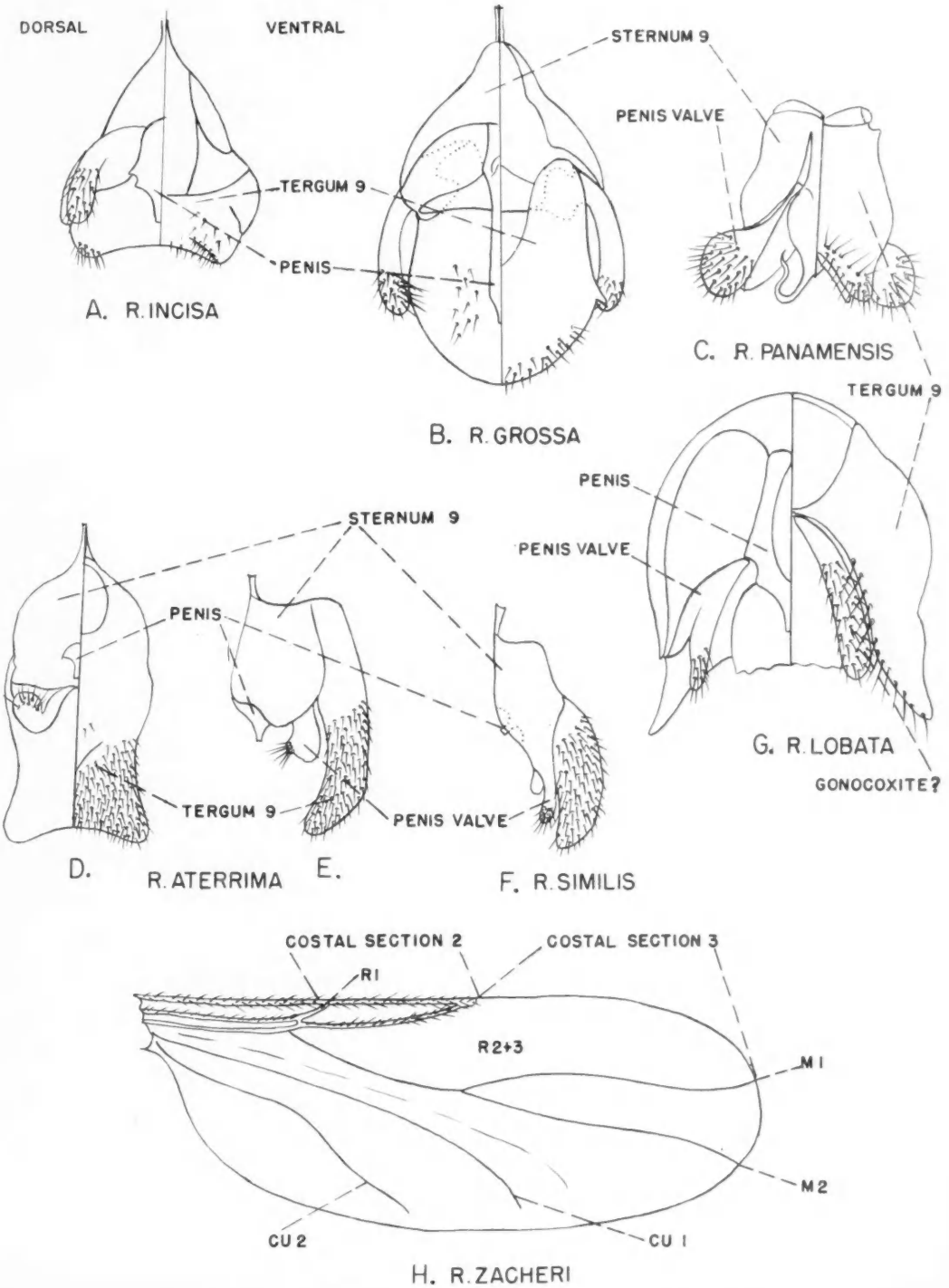

FIG. 1. Male genitalia of *Rhexoza, Zacheri* group, and wing of *R. zacheri*.

with a pair of minute, setaceous appendages. Cerci small; spermatheca spherical.

Dampfi Group

These are characterized in the males by the production of tergum 9 (or the gonocoxites) into a long, curved, pointed or a short, straight median process ventrad of the heavily sclerotized penis (fig. 5A, B), with either a single pair of appendages (penis valves) or none. The only species of which the female is known has sternum 8 produced into two contiguous, posteriorly directed, triangular processes, and tergum 8 completely divided medially (fig. 5E).

The two species constituting this group are vastly different in size, *R. dampfi* up to 2.75 mm. long and *R. cryptica* only 1.30 mm. long.

KEY TO THE SPECIES GROUPS IN THE GENUS RHEXOZA BASED ON KNOWN AMERICAN SPECIES

1. Male genitalia laterally compressed, with tergum 9 produced ventrally in a beak-like process (fig. 4A, B, C). Female genitalia with tergum 8 medially divided, sternum 8 not produced posteriorly (fig. 4E, F) ..... **Quatei** Group
1a. Male and female genitalia not as above 2
2. Male genitalia with tergum 9 (located ventrally) drawn into a longer or shorter median, pointed process (fig. 5A, B) immediately beneath the large, well sclerotized penis. Female genitalia with sternum 8 produced into two posteriorly directed, adjacent, conical processes (fig. 5E) ..... **Dampfi** Group
2a. Male genitalia not as above, tergum 9 incised or rounded but not apically acute. Female genitalia with sternum 8 not produced into acute lobes posteriorly ..... **Zacheri** Group

KEY TO THE KNOWN AMERICAN SPECIES OF RHEXOZA, ZACHERI GROUP

Males (*R. zacheri*, European species, ♂ unknown.)

1. Tergum 7 produced posteriorly into two large lobes (fig. 2F) ..... **lobata**
1a. Tergum 7 not so produced 2
2. Tergum 7 medially incised (fig. 2B); size large (2.38–2.70 mm.) ..... **grossa**
2a. Tergum 7 not incised medially; size smaller (2.00 mm. or less) 3
3. Tergum 7 produced posteriorly as an acute or obtuse median lobe (fig. 2D, E) 4
3a. Tergum 7 not produced posteriorly, may be emarginate or sinuate (fig. 2A, C) 5
4. In northeastern United States and southeastern Canada; supra-alar setae numerous (21), in a double row anteriorly; male genitalia as in fig. 1F ..... **similis**
4a. From Rocky Mts. to Pacific Coast; supra-alar setae fewer (11–13), in a single row; male genitalia as in fig. 1D, E ..... **aterrima**
5. Tergum 7 emarginate posteriorly (fig. 2C); section 3 of costal margin 3.5 times as long as section 2 ..... **panamensis**
5a. Tergum 7 posteriorly sinuate (fig. 2A); section 3 of costal margin less than 2.5 times as long as section 2 ..... **incisa**

Females (♀ of *R. lobata* unknown)

1. Tergum 8 longitudinally divided, with setae on anterior margin (fig. 3D) ..... **grossa**
1a. Tergum 8 entire, no anterior setae 2
2. Sternum 8 entire but medially incised (fig. 3C, F) .. 3
2a. Sternum 8 divided longitudinally 4
3. Sternum 8 with a large triangular incision in posterior margin (fig. 3C) ..... **panamensis**
3a. Sternum 8 with a broad, shallow, posterior emargination (fig. 3F) ..... **aterrima**
4. Tergum 8 bilobed, with a deep posterior emargination (fig. 3B) ..... **incisa**
4a. Tergum 8 but slightly emarginate posteriorly (fig. 3E) ..... **similis**

KEY TO KNOWN AMERICAN SPECIES OF QUATEI GROUP

Males

1. Posterior processes of tergum 8 with a basal tooth ventrally (fig. 4G); tergum 9 without dorsally projecting horns (fig. 4C) ..... **quatei**
1a. Posterior processes of tergum 8 without a basal tooth (fig. 4D); tergum 9 with paired, dorsally projecting, hornlike processes posteriorly (fig. 4B) ..... **miniscula**

Females: Only separable by examination of genitalia (fig. 4E, F), and by distribution. *R. quatei*, as far as known, is limited to California; *R. miniscula* from Texas to the east coast.

Species of Dampfi Group

The two species here are readily separated by size and color differences. *R. cryptica* is 1.30 mm. long or less and largely dull grey-brown in color. *R. dampfi* is larger, up to 2.75 mm. long, with the terminal abdominal segments bright yellow brown or orange.

Rhexoza zacheri Enderlein

Rhexoza zacheri Enderlein, 1936. Die Tierwelt Mitteleuropas, 6, Lief. 2, Inseckten 3: 55. Type species of the genus.

Female: Total length 2.00 mm. Dark grey-brown, dull; head black; antennae dull black; abdomen dull; halteres grey; femora with broad medial lighter grey-brown band; tibiae of pro- and mesothoracic legs with a similar band displaced somewhat distally; tibiae of metathoracic legs paler on apical two-thirds; tarsi paler grey-brown.

Maxillary palpi 0.12 mm. long. Enlarged supra-alar setae in a definite row, 8 in number; 12 subspiracular setae; 5 setae on pedicel of halter.

Wings (fig. 1H) 1.55 mm. long. Section 3 of costal margin 2.33 times as long as section 2; M_1 1.75 times as long as M.

Genitalia as in fig. 3A.

This species is European but has apparently not been recorded since Enderlein's original description.

Specimen examined: One ♀, Berlin, May 15, 1918, aus Faülenden Kartoffeln. Dr. Zacher. This apparent holotype ♀ is in the collection of the Zoological Museum of the University of Berlin.

Rhexoza aterrima (Melander), new comb.

Rhegmoclema aterrima Melander, 1916. State Coll. Wash. Ag. Exp. Sta. Bull. 130, p. 14, Fig. 15.

Males: Total length 1.55–1.65 mm. Color dark brownish black; head and mesonotum jet

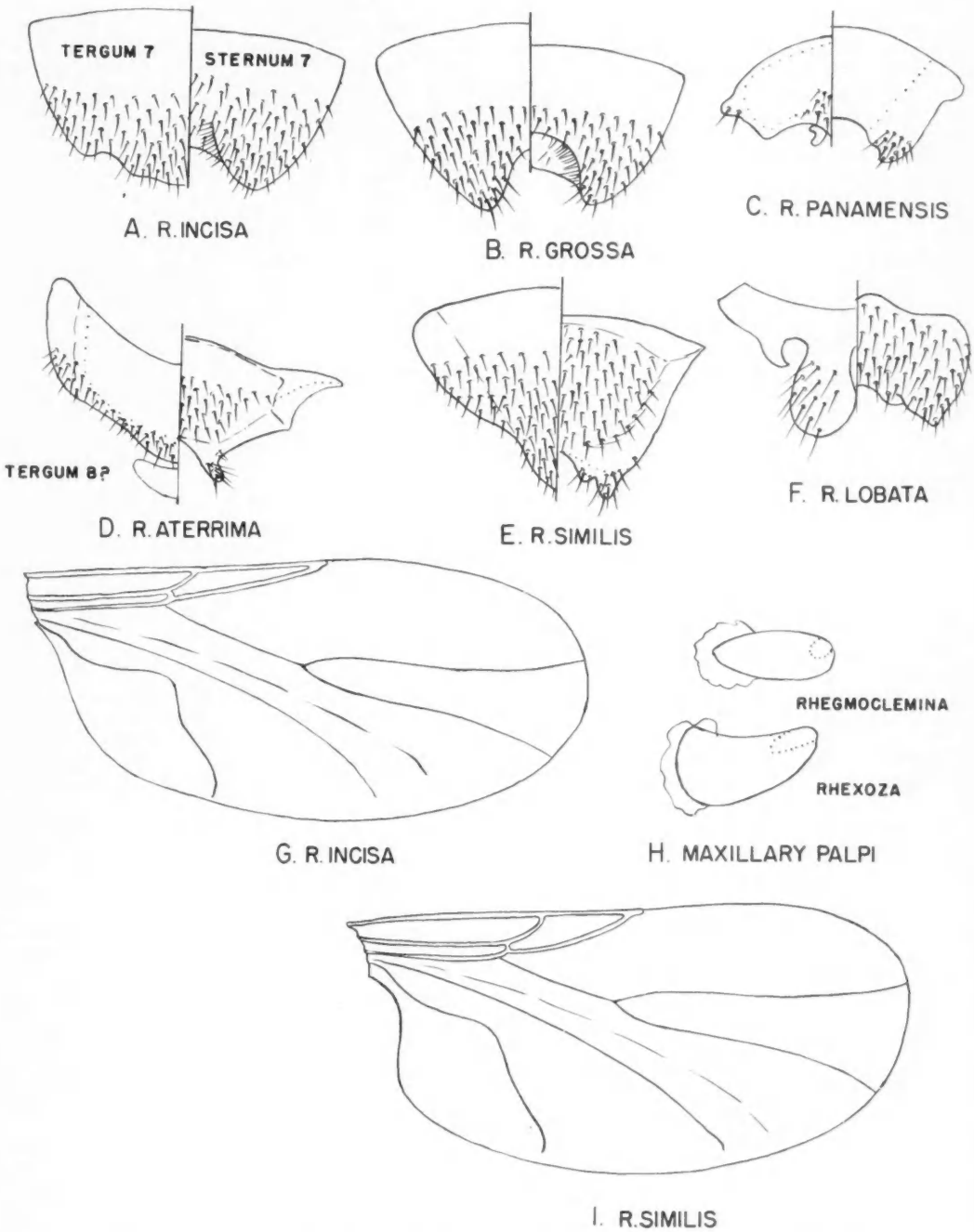

FIG. 2. Seventh segment of males, maxillary palpi, and wings of *Rhexoza* spp., *Zacheri* group.

black, somewhat shining; antennae dull black; abdomen feebly shining dorsally, dull ventrally; halteres dark grey; tarsi concolorous with body or slightly paler, covered with silvery pubescence; empodia white. Maxillary palpi 0.10–0.12 mm. long. Supraalar setae 11–13; 2–5 subspiraculars; 1–4 setae on pedicel of halter.

Wings 1.24–1.50 mm. long. Section 3 of costal margin four times as long as section 2; M_1 2.2 times as long as M.

Segment 7 of abdomen as in fig. 2D. Genital vesica and apodemes 0.17–0.20 mm. long. Genitalia as in fig. 1D, E.

Females: Total length 1.35–2.00 mm. Wing length 1.35–1.58 mm. Supra-alar setae 10; 1 subspiracular; 1 seta on pedicel of halter. Tergum 1 with single row of setae on posterior margin only. Genitalia as in fig. 3F. Sternum 8 deeply incised but entire; tergum 8 entire. Cerci small, concolorous with abdomen or slightly paler. Otherwise as male in color and chaetotaxy.

This species was originally described from a single female. On the basis of the male and female genitalia it is most closely related to *R. similis*.

Collected in Idaho, Montana and California.

Specimens examined: Holotype: ♀, Chatcolet Lake, Idaho, Aug. 1915, A. L. Melander. Holotype in collection of A. L. Melander. Three ♂♂, 1♀, Berkeley, Calif., Apr. 17–25, 1948; 1♀, Berkeley, May 1, 1948; 1♂, Coeur d'Alene, Idaho, June 18, 1932, off *Pinus ponderosa;* 1♂, Lake Waha, Idaho, June 9, 1948; 3♀♀, Coeur d'Alene, Idaho, Aug. 24, 1916; 1♀, Three Forks, Montana, Aug. 1, 1918.

Rhexoza similis (Beekey), new comb.

Scatopse similis Beekey, 1938. Ent. News 49: 151–154.

Males: Total length 1.90–2.00 mm. Color dark brown to black, feebly shining on head and scutum, abdomen dull; posterior abdominal segments darker on posterior half, giving a ringed appearance; antennae dull black; halteres dark grey to black; tarsi concolorous with or somewhat paler than body, more grey than brown; empodia white. Maxillary palpi 0.12 mm. long. Supra-alar setae 21, in a double row anteriorly; 8 subspiraculars, 5 large, 3 small; 3 setae on pedicel of halter.

Wings 1.50–1.70 mm. long. Section 3 of costal margin 3.5 times as long as section 2; M^1 2.25 times as long as M (fig. 21).

Segment 7 of abdomen as in fig. 2E. Genital vesica and apodemes 0.25 mm long. Genitalia as in fig. 1F.

Females: Total length 1.62–2.20 mm. Wing length 1.20–1.62 mm. Supra-alar setae 14–15; 7 subspiraculars; 2–3 setae on pedicel of halter. Tergum 1 of abdomen with a single row of setae on posterior margin and a few anteriorly in middle. Genitalia as in fig. 3E. Tergum 8 entire; cerci somewhat paler than abdomen and larger than in *R. aterrima*. Sternum 8 entirely divided longitudinally. Otherwise as male in color and chaetotaxy.

The larva of this species has been described and illustrated by Beekey. This will be redescribed in a subsequent paper on the immature stages of the group. The larvae and pupae were found beneath the loose bark of spruce logs floating in the Penobscot River near Orono, Maine.

Specimens examined: Five ♂♂, 1♀, paratypes, Orono, Maine, Oct. 20, 1909; 2♀♀, Trenton, Ontario, June 16–17, 1901; 1♀, Great Whale R., Quebec, July 26, 1949; 1♀, Constance B., Ontario, 3–I–52 [sic].

Types in Cornell University Collection.

Rhexoza grossa n. sp.

Males: Total length 2.38–2.60 mm. Color dark brownish black, feebly shining; head jet black; antennae dull black with silvery white pubescence; sides of thorax grey-brown, shining; legs concolorous with body, except tarsi paler, dark greyish yellow; halteres dark grey; empodia white; setae of head and thorax black, posterior abdominal setae silvery. Maxillary palpi 0.15 mm. long. Supra-alar setae 12; subspiraculars 10; 2 setae on pedicel of halter.

Wings 1.90–1.96 mm. long. Section 3 of costal margin 2.8 times as long as section 2; M_1 twice as long as M.

Segment 7 of abdomen as in fig. 2B. Genital vesica and apodemes 0.29 mm. long. Genitalia as in fig. 1B.

Females: Total length 2.58–2.80 mm. Wing length 1.86–2.00 mm. Supra-alar setae 14; subspiraculars 15; 3–4 setae on pedicel of halter. Tergum 1 of abdomen with numerous setae in addition to the posterior marginal row. Genitalia as in fig. 3D. Cerci much larger than in other species, concolorous with abdomen. Tergum 8 divided longitudinally; sternum 8 also divided. Otherwise as male in color and chaetotaxy.

Specimens are available only from California and Oregon.

Specimens examined: Holotype: ♂, Del Puerto Canyon, Stanislaus Co., Calif., May 11, 1948, Ray F. Smith, from *Eriodictyon* (Yerba Santa). Slide mount. In University of California Collection. Allotype: ♀, Corvallis, Oregon, Aug. 11, no other data. Slide mount. In the Oregon State College Collection. Paratypes: 1♂, 3♀♀, same data as allotype.

Rhexoza incisa n. sp.

Males: Total length 1.38–1.86 mm. Color dark brown to jet black; head and mesonotum shining; antennae dull black with silvery pubescence; abdomen dull laterally, feebly shining dorsally; sides of thorax brown, shining; tergum 7 may be paler brown to yellowish or concolorous with rest of abdominal terga; legs paler, grey or brown; halteres dark grey to black; empodia white. Maxillary palpi 0.10–0.12 mm. long.

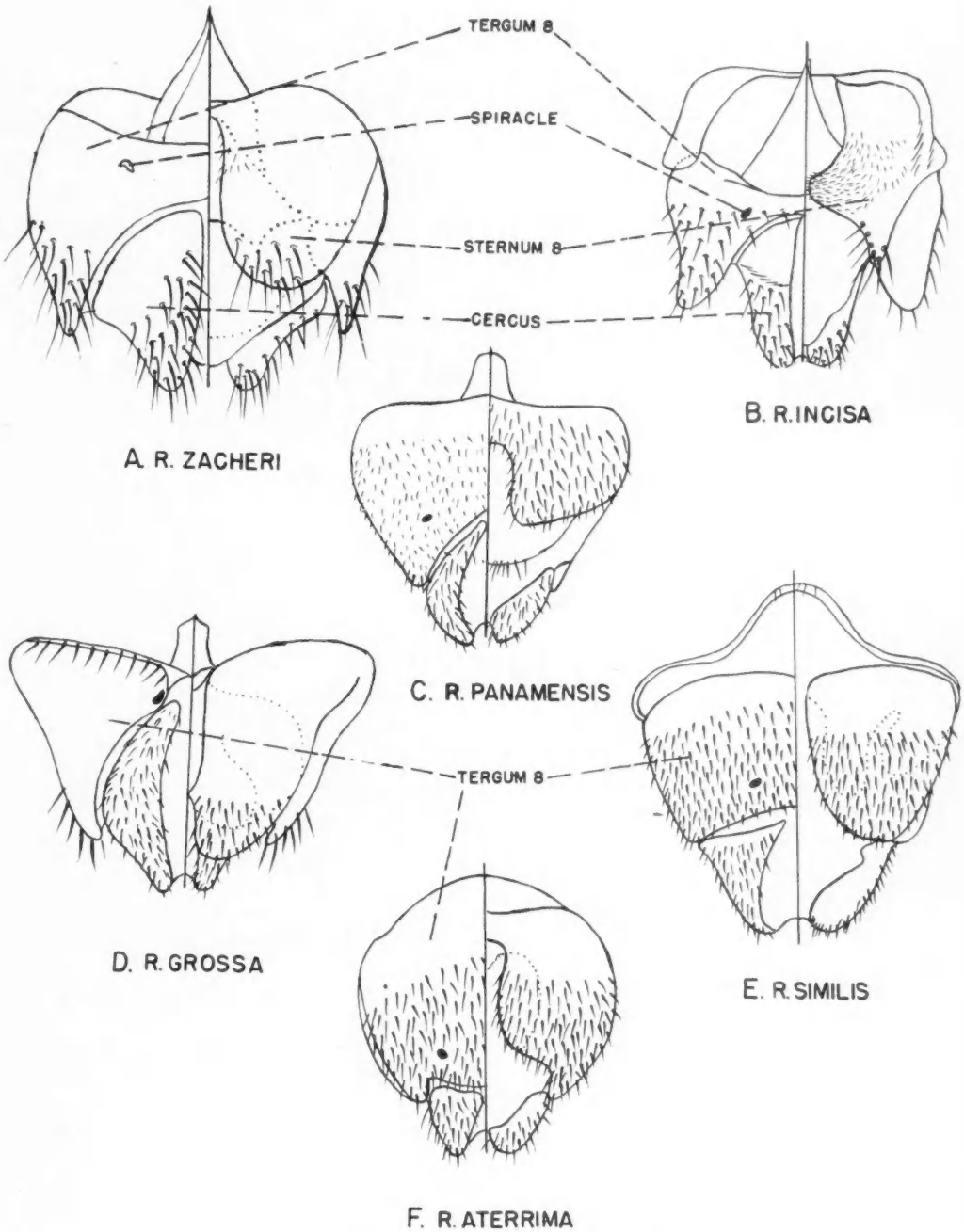

FIG. 3. Female genitalia of *Rhexoza, Zacheri* group.

Supra-alar setae 16–20; subspiraculars 4–9; 1–3 setae on pedicel of halter.

Wings 1.27–1.48 mm. long. Section 3 of costal margin 2.3 times as long as section 2; M_1 2.5 times as long as M (fig. 2G).

Segment 7 of abdomen as in fig. 2A. Genital vesica and apodemes 0.24–0.27 mm. long. Genitalia as in fig. 1A.

Females: Total length 1.62–2.06 mm. Wing length 1.27–1.68 mm. Supra-alar setae 11–17; subspiraculars 5–7; 1–3 setae on pedicel of halter. Tergum 1 of abdomen with a few setae medially and anteriorly in addition to the posterior marginal row. Genitalia as in fig. 2B. Tergum 8 entire but deeply incised; sternum 8 completely divided longitudinally. Cerci large, reddish-yellow. Otherwise as male in color and chaetotaxy.

Close to *R. grossa* in both male and female genitalia.

The larvae of this species have been collected from beneath the bark of dead American elm, box elder, and cottonwood trees at St. Paul, Minn. and Champaign and Urbana, Ill. Those collected at Urbana in Sept. 1948 in cottonwood emerged as adults May 7–12, 1949. Those collected on Dec. 3 in box elder in Champaign emerged as adults on Dec. 31. Larvae were also collected in dead box elder on Jan. 9 at Champaign. Larvae were collected in a dying American elm at St. Paul, Minn., on April 24, 1952 by B. Ebel, and these emerged as adults on May 2–6, 1952. The larva will be described in a subsequent paper.

Several of the adults that were reared from larvae collected in St. Paul failed to expand their wings. This resulted in a vestigial-winged appearance.

This species has been collected in Iowa, Illinois, Minnesota and Ontario.

Specimens examined: Holotype: ♂, St. Paul, Minn., under bark of American elm, collected as larva April 24, 1952, emerged as adult May 6, 1952, B. Ebel. *Allotype:* ♀, same data. Holotype and allotype in University of Minnesota Collection. Slide mounts. *Paratypes:* 5♂♂, 7♀♀, same data; 1♀, Ft. Snelling, Minn., April 28, 1952; 17♂♂, 7♀♀, Champaign, Ill., Dec. 3, 1948; 2♀♀, Urbana, Ill., May 7–12, 1949; 5♂♂, 3♀♀, Ames, Iowa, May 14–28, 1951; 3♀♀, Ames, Iowa, April 4, 1952; 1♀, Des Moines, Iowa, May 5, 1951; 2♂♂, Marmora, Ontario, July 31, 1952.

Rhexoza panamensis n. sp.

Males. Total length 1.90–2.00 mm. (approx.). Head, antennae, thorax and abdomen dark grey-brown; palpi grey; thorax subshining, rest of body dull; halteres dark grey; tarsi pale yellowish; all setae dark brown. Maxillary palpi 0.10–0.12 mm. long. Supra-alar setae 11–15; subspiraculars 6–7; 2–3 setae on pedicel of halter.

Wings 1.2 mm. long. Section 3 of costal margin 3.5 times as long as section 2; M_1 2.8 times as long as M.

Segment 7 of abdomen as in fig. 2C. Genital vesica and apodemes 0.18–0.24 mm. long. Genitalia as in fig. 1C.

Females: Total length 2.00 mm. (approx.). Wings 1.3 mm. long. Supra-alar setae 13; subspiraculars 7; 3 setae on pedicel of halter. Tergum 1 of abdomen with scattered setae at sides and an anterior and posterior row. Female genitalia as in fig. 3C. Spermatheca elongate. Cerci concolorous with abdomen. Both tergum and sternum 8 entire, much like *R. similis*. Otherwise as male in color and chaetotaxy.

Specimens examined:

Holotype: ♂, Ancon, Canal Zone, June 1, 1923. Allotype: ♀, same data. Types in the U. S. National Museum. Slide mounts. Paratype: ♂, Canal Zone, on burlap bag of raw rubber, April 30, 1943.

Rhexoza lobata n. sp.

Male: Total length 1.90 mm. Color dark grey-brown; head and mesonotum black, feebly shining, rest of body dull; antennae dull black; tarsi paler, yellowish; halteres dark grey. Maxillary palpi 0.12 mm. long. Supra-alar setae 9; subspiraculars 5; 4 on pedicel of halter.

Wings 1.7 mm. long; section 3 of costal margin 2.5 times as long as section 2; M_1 2.6 times as long as M.

Segment 7 of abdomen as in fig. 2F. Genitalia as in fig. 1G. The genitalia of the only specimen of this species available are somewhat damaged. It can be observed in the illustration that the median sclerite beneath the penis has been broken off.

Female: Unknown.

This species is most closely related to *R. panamensis* on the basis of the male genitalia.

Specimens examined:

Holotype: ♂, Cordoba, Vera Cruz, Mexico, May 14, 1908, A. Fenyes. Type in U. S. National Museum Collections. Slide mount.

Rhexoza quatei n. sp.

Males: Total length 1.20–1.55 mm. Color dark grey-brown to black, feebly shining; head and mesonotum no darker; antennae dull black with silvery pubescence; maxillary palpi grey to black; halteres dark grey; anterior abdominal terga may be paler brown; meso- and methathoracic tarsi paler, yellowish grey basally (not so in specimens from central California); prothoracic tarsi dark grey-brown; supra-alar and scutellar setae black; all other setae yellowish, pale. Maxillary palpi 0.12 mm. long. Supra-alar setae 10–13; subspiraculars 3–5; 2–3 setae on pedicel of halter.

Wings 1.00–1.20 mm. long (fig. 4H). Section

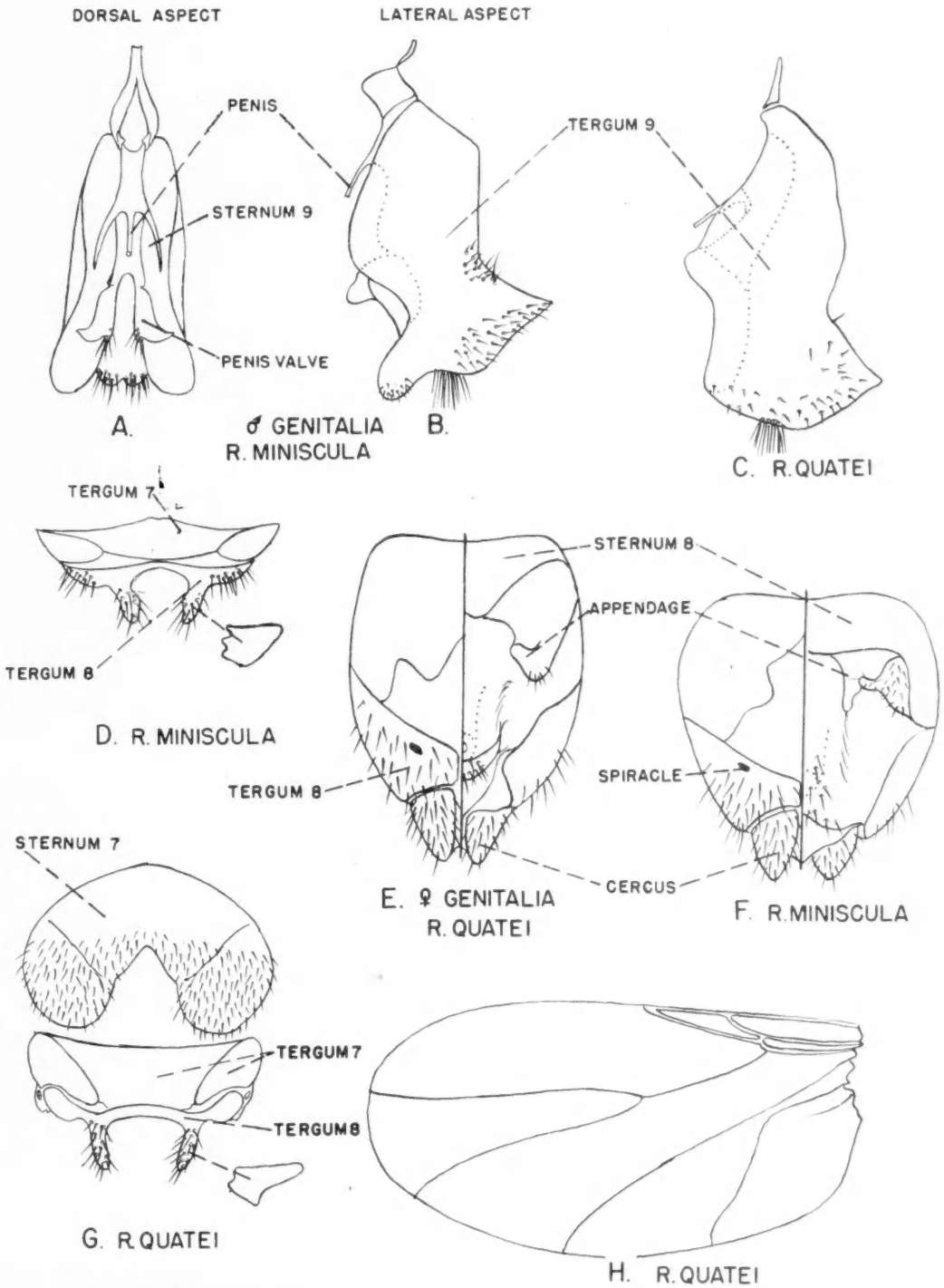

FIG. 4. Male seventh segment, male genitalia, female genitalia, and wing of *Rhexoza* spp., *Quatei* group.

3 of costal margin four times as long as section 2; M_1 twice as long as M.

Segments 7 and 8 of abdomen as in fig. 4G. Genital vesica and apodemes 0.12–0.13 mm. long. Genitalia as in fig. 4C.

Females: Total length 1.80–2.14 mm. Wing length 1.30–1.38 mm. Supra-alar setae 10–18; subspiraculars 4–7; 1–2 setae on pedicel of halter. Genitalia as in fig. 2E; cerci concolorous with abdomen. Otherwise as male in color and chaetotaxy.

Specimens examined.

Holotype: ♂, Davis, California, Oct. 15, 1952, J. C. Hall. Allotype: ♀, same data. Types slide mounted and deposited at the University of California College of Agriculture at Davis, California. Paratypes: 5♀♀, Davis, Calif., Oct. 15–27, 1952; 4♂♂, 9♀♀, Riverside, Calif., Jan. 12, 1935; 2♂♂, 1♀, Coachella, Calif., June 7, 1931; 2♂♂, 2♀♀, Rialto, San Bernardino Co., Calif., June 11, 1950, citronella trap; 1♂, Anaheim, Calif., Aug. 11, 1950, citronella trap; 1♂, Olive, Orange Co., Calif., Aug. 7, 1950, citronella trap.

Rhexoza miniscula n. sp.

Males: Total length 1.30–1.74 mm. Dark grey-brown; head and sometimes mesonotum black, feebly shining; antennae dull black, second segment paler brown; maxillary palpi paler grey; sides of thorax lighter brown; tarsi of meso- and methathoracic legs paler, yellowish grey basally; prothoracic tarsi colored as body; halteres dark grey. Maxillary palpi 0.10 mm. long. Supra-alar setae 9–11; subspiraculars 5–7; 1–4 on pedicel of halter.

Wings 1.00–1.24 mm. long. Section 3 of costal margin 3.5 times as long as section 2; M_1 twice as long as M.

Terga 7 and 8 of abdomen as in fig. 4D; sternum 7 like that of *R. quatei*. Genital vesica and apodemes 0.18 mm. long, larger than in *R. quatei*. Genitalia as in fig. 4A, B.

Females: Total length 1.55–1.97 mm. Wing length 1.10–1.38 mm. Supra-alar setae 9–10; subspiraculars 7; 1–2 on pedicel of halter. Genitalia as in fig. 4F. Cerci somewhat paler than abdomen. Otherwise as male in color and chaetotaxy.

Specimens examined:

Holotype: ♂, Gate City, Virginia, Aug. 11, 1911, bred from cucumber stems. Allotype: ♀, same data. Types slide mounted and deposited in the U. S. National Museum Collections. Paratypes: 1♂, 1♀, same data as above; 1♂, 2♀♀, Churchland, Virginia; 2♂♂, Batesburg, South Carolina, issued Aug. 1, 1924, in melon roots; 2♂♂, 3♀♀, Dallas, Texas, Oct. 24, 1912; 1♀, Uvalde, Texas, April 11, 1914; 1♀, Victoria, Texas, April 18, 1908.

Rhexoza dampfi (Duda), new comb.

Scatopse dampfi Duda, 1928. Konowia, 7: 280–282, Fig. 11, Taf. IV, Fig. 3.

Males: Total length 2.22–2.75 mm. Dark grey-brown in general, membranes between sclerites white; head jet black, shining at sides; mouthparts grey, maxillary palpi white mesally; antennae dull black, covered with silvery pubescence; thorax grey-brown dorsally, feebly shining, muscle origins paler, margined with black; pleural areas grey-brown, shining; scutellar and supra-alar setae black, the rest pale brown; prothoracic legs largely dark grey-brown, meso- and methathoracic legs paler, yellowish grey, dark only on mesal face and apices of femora; dark narrow band at middle and distal ends of tibiae; terminal segments of tarsi dark; halteres dark grey on outer face, pale grey on inner; abdomen shining grey-brown on first 4 segments dorsally, darker dull brown on segments 5 and 6, segment 7 pale yellow- or orange-brown; segments 1–6 dull grey-brown ventrally and laterally, sternum 7 yellow- or orange-brown as tergum.

Maxillary palpi 0.17 mm. long. Supra-alar setae 13–19; subspiraculars 10–14; 4–6 setae on pedicel of halter.

Wings 1.90–2.17 mm. long; section 3 of costal margin four times as long as section 2; M_1 twice as long as M.

Segments 7 and 8 of abdomen as in fig. 5C. Genital vesica and apodemes 0.22 mm. long. Genitalia as in fig. 5B.

Females: Total length 2.08–2.72 mm. Wing length 1.90–2.28 mm. Supra-alar setae 25–27; subspiraculars 21; 3–5 setae on pedicel of halter. Genitalia as in fig. 5E. Sternum 8 drawn out into two posteriorly directed processes. Tergum 8 completely divided by cerci. Tergum 7 and genitalia pale orange- or yellow-brown. Otherwise as male in color and chaetotaxy.

This is by far the largest and most brightly colored species of this genus yet seen.

Specimens examined:

Three ♂♂, 2♀♀, Popotea [Mexico], Jan. 15, 1925; 24♂♂, 15♀♀, Mexic. at Brownsville, Texas [sic], April 21, 1948; 1♂, trans Mexico at San Antonio, Texas, May 13, 1945; 2♂♂, 1♀, trans Mexico at Laredo, Texas, Jan. 11, 1941, chrysanthemums.

Rhexoza cryptica n. sp.

Males: Total length 1.13–1.31 mm. Dull grey-brown; head jet black, shining; antennae dull black; thorax grey-brown, feebly shining; legs largely concolorous with thorax except a paler ring in middle of tibiae, tarsi paler yellowish grey; halteres dark grey; abdomen dull grey-brown; setae all yellowish brown except scutellars and supra-alars black. Maxillary palpi 0.10 mm. long. Supra-alar setae 7–8; subspiraculars 1–2; 2–4 small setae on pedicel of halter.

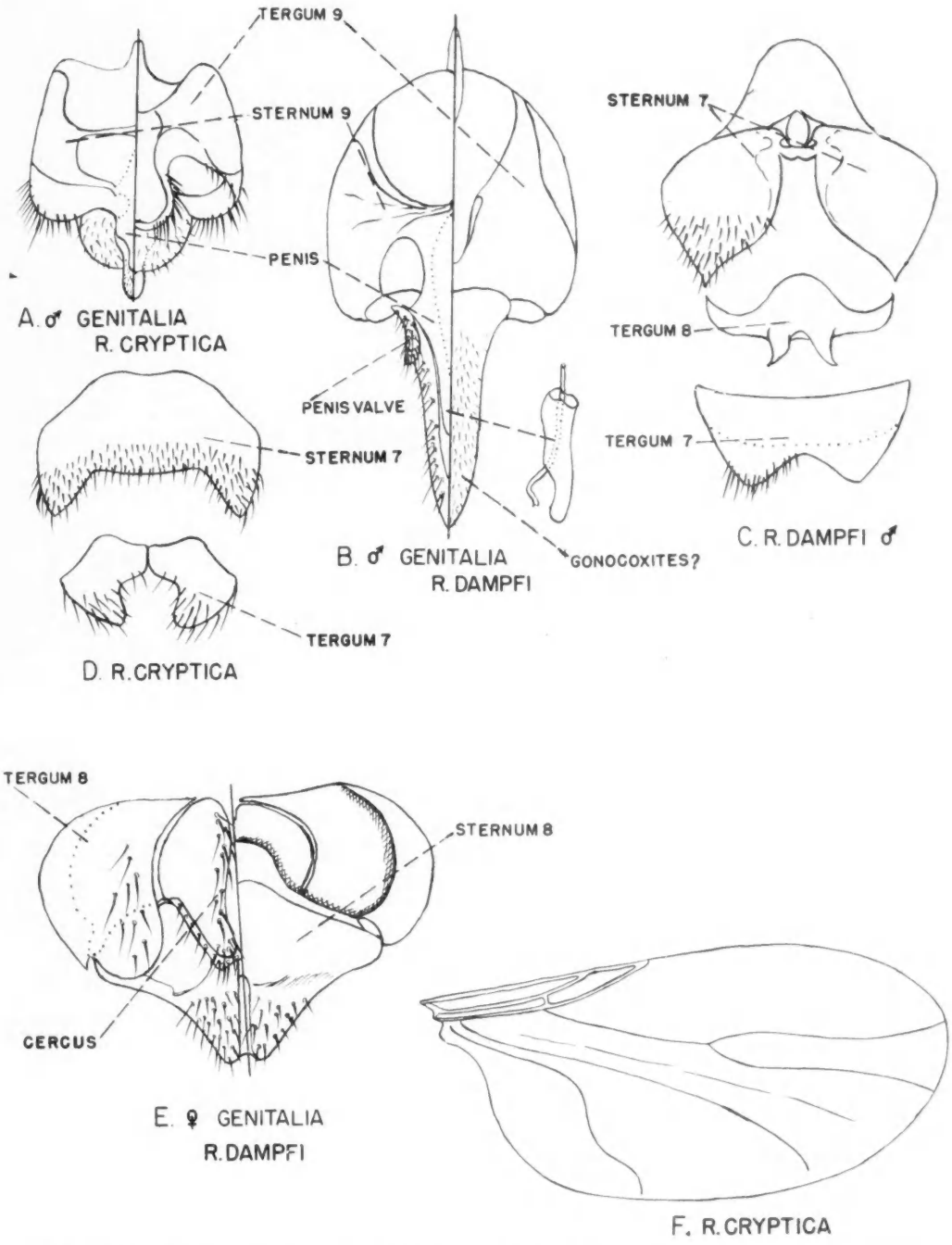

FIG. 5. Male seventh segment, male genitalia, female genitalia, and wing of *Rhexoza* spp., *Dampfi* group.

Wings (fig. 5F) 1.10–1.14 mm. long. Section 3 of costal margin seven or more times as long as section 2; M_1 1.6 times as long as M.

Segment 7 of abdomen as in fig. 5D. Genital vesica and apodemes 0.29–0.36 mm. long. Genitalia as in fig. 5A.

Female: Unknown.

Comments:

This species differs from the species with which it is here associated, *R. dampfi*, in a number of particulars. Segment 8 is apparently entirely lacking; the genital vesica and apodemes are larger; section 2 of the costal margin is quite short, approaching the condition in *Swammerdamella;* and the thorax shorter and broader than any considered so far in this study. The two species are associated solely on the very similar structure apparent in the male genitalia.

Specimens examined:

Holotype: ♂, Falls Church, Virginia, April, 1951, W. W. Wirth, Holmes Run, ex. debris in tree crotch. Slide mounted. Holotype in collection of the U. S. National Museum. Paratypes: 5♂♂, same data.

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EFFECTS OF TEMPERATURE AND PARENTAL AGE ON THE LIFE CYCLE OF THE MEALWORM, TENEBRIO MOLITOR LINNAEUS (COLEOPTERA, TENEBRIONIDAE)

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The number of molts in an insect may be constant regardless of environmental factors. This condition occurs in the Japanese beetle, *Popillia japonica* (Ludwig, 1928).

On the other hand, a rise in temperature may increase the number of molts. Przibram and Megusar (1912) found that in the praying mantis, *Sphodromantis bioculata*, the number changed from 9 to 11 as temperature increased from 25° to 37° C. Kreyenberg (1929) observed that larvae of the beetle, *Dermestes lardarius*, had 5 molts in the male and 6 in the female at 28° C., while at lower temperatures the numbers were 4 and 5, respectively. Gierke (1932) reported that the larvae of the meal moth, *Ephestia kühniella*, molted 5 times at 25°, and 4 times at 18° C.

Temperature may also have the reverse effect as shown by the work of Parker (1930), who observed that the grasshopper, *Melanoplus mexicanus*, molted 6 times at 22° to 27° C. and only 5 times at 32° to 37° C.; and of Klein (1932) who showed that larvae of the butterfly, *Pieris brassicae*, had 3 molts at temperatures of 22° to 27°, 4 between 15° and 20°, and 5 at 14° to 15° C. Lengerken (1925) kept larvae of the mealworm, *Tenebrio molitor*, in a cold room and found that the larval period was increased by several months and there were many supernumerary molts. Cotton (1927) observed that the number of molts in this insect varied from 9 to 20 with half of the larvae molting 17 to 19 times. In this work no reference was made to the effects of temperature on molting. Because of the variation in the number of molts described by Cotton, it was decided to rear larvae of *T. molitor* at the constant temperatures of 25° and 30° C. to determine whether temperature might also be an important factor controlling the frequency of ecdysis in this species.

Accepted for publication, May 3, 1955.

MATERIAL AND METHODS

Eggs of the mealworm were obtained from beetles kept in white flour. They were collected daily and put in desiccators, the bases of which contained a saturated solution of NaCl (relative humidity, 75 per cent) and were incubated at 30° C. In one series of experiments, larvae within 24 hours of eclosion were placed individually in 2 ml. vials containing enough chick growing-mash to supply ample food but not enough to enable the larvae to bury themselves. This procedure made possible the observation of the very small larvae without difficulty. As the larvae grew larger, they were transferred to larger vials with an increased amount of food. A drop of water was added to the mash each day. These larvae were kept at 25° or at 30° C. and examined daily until after pupation. When a larva had molted, the exuvium was removed from the vial and the date of ecdysis was recorded. In this manner an exact record of the number of larval molts and the duration of each instar was obtained for each insect. In a second series of experiments, groups of newly hatched larvae were placed in dated beakers containing an

abundance of food and placed at 25° or at 30° C. Water was also added daily. They were allowed to complete their development and the dates of hatching and of pupation were recorded for each insect.

OBSERVATIONS

There is considerable variation in the number of molts during the larval stage of *Tenebrio molitor*. Furthermore, the frequency of molting is dependent on temperature. Larvae kept singly at 25° C. molted from 11 to 15 times, with an average of 13.2; and those at 30° C., from 15 to 23 with an average of 19.1 times. This effect of temperature is shown in Figure 1. The average duration of each instar is plotted in Figure 2. Larvae kept at 25° required a longer time between molts than for the corresponding molts in those at 30° C., but since fewer molts occurred at the lower temperature, the larval stage was completed in a shorter time. Early in larval growth the duration of each instar was relatively short, but towards the end of larval life, the time between molts was greatly increased, lasting from 2 to 3 weeks at the lower temperature, and from 3 to 5 weeks at the higher temperature. Figure 2 also shows that the average duration of the first instar was longer than that of the second to tenth at 25° and the second to fourteenth at 30° C. At each temperature the average duration of the last instar was considerably shorter than the maximal values.

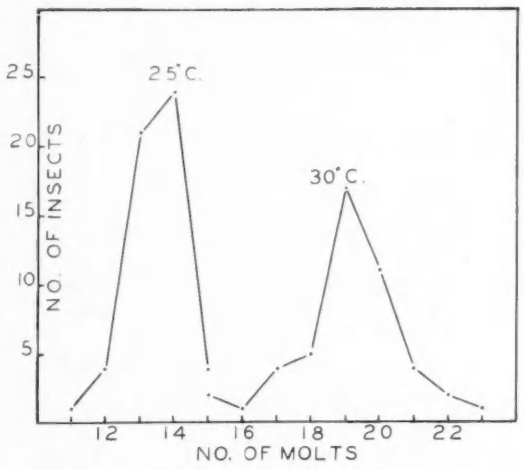

FIGURE 1. Number of larval molts for specimens held singly at the constant temperatures of 25° and 30° C.

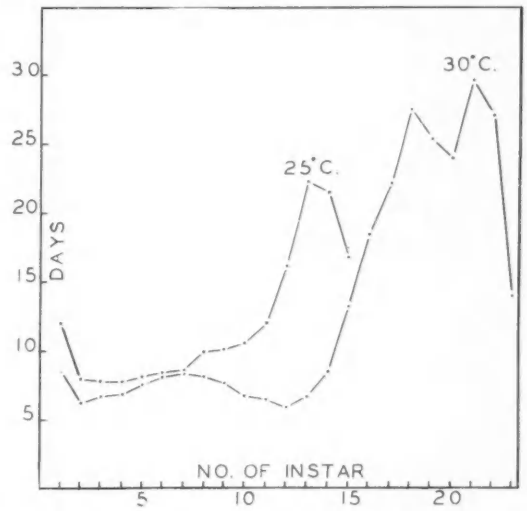

FIGURE 2. Average duration of each larval instar for specimens kept singly at the constant temperatures of 25° and 30° C.

Larvae reared in groups at 30° C were obtained from beetles of different ages. One group of eggs placed at this temperature was obtained from newly emerged adults. These beetles were then used to supply eggs for rearing experiments at 25° C., and later (more than 1 month after the first collections grown at 30°) they also supplied eggs for additional rearing experiments at 30° C. Thus, although no effort was made to determine the age of beetles used for egg-laying, it appears from figures given in Table 1 that parental age influences the duration of the larval stage. The table shows that larvae from newly emerged beetles and reared in groups required an average of approximately 187 days, whereas those from older beetles required only 160 days in the larval stage. Temperature was also important in determining the duration of larval life. As shown in Figure 2, the duration of the larval stage was shorter at 25° than at 30° C. for larvae kept singly in vials. The figures in Table 1, obtained from larvae kept in groups, also show that larval life was shorter at the lower temperature. Grouping of the larvae appears to be important in modifying the duration of the larval stage. At 25° C. the average value was approximately the same in grouped larvae as in those reared singly. However at 30° C., larvae reared individually required a significantly longer time (213 days) in the larval stage than did those reared in groups (187 days).

DISCUSSION

These observations indicate that temperature is a very important factor in determining the number of molts in the mealworm, *T. molitor*. Previous workers (Przibram and Megusar, 1912; Severin and Severin, 1913; Kreyenberg, 1929; Parker, 1930; Gierke, 1932; and Klein, 1932)

have observed that changes in temperature modify the number of molts in certain insects, but the modifications consisted of only one or two molts as temperature was changed approximately 10° C. Hence, the effects reported here (11 to 15 molts at 25°, and 15 to 23 at 30°) are much greater than those reported for any other insect. It seems likely that the variations in the number of molts in this species (9 to 20) observed by Cotton (1927) may have been caused, at least in part, by temperature changes. The increase in the number of molts obtained by Lengerken (1925) when larvae of this species were kept in a cold room may have been caused by factors other than temperature. The temperature may have been low enough to produce periods of inactivity and partial starvation. This latter factor is known to increase the number of molts in insects (Calvert, 1929).

TABLE I

DURATION OF THE LARVAL STAGE

CONDITION OF EXPERIMENT	NO. OF LARVAE	DURATION OF LARVAL STAGE IN DAYS (with standard errors)
Larvae reared in groups at 25° C.	477	148±1.00
Larvae reared singly at 25° C.	54	152±2.34
Larvae reared in groups at 30° C.		
Eggs from young parents	157	187±2.63
Eggs from old parents	72	160±3.38
Larva reared singly at 30° C.		
Eggs from young parents	48	213±6.35

The beneficial effects obtained by grouping the larvae at 30° C. are comparable to the results of Chauvin (1946) who found that nymphs of the cockroach, *Blattella germanica*, in groups of 5 increased in weight more rapidly than those kept singly. He postulated that the excreta mixed with food exercise an accelerating effect on growth.

The influence of parental age on the duration of the life cycle is in agreement with the work of Jennings and Lynch (1928) and of Lansing (1954) on rotifers. Lansing found that the longevity of the rotifer, *Philodina citrina*, increased in an adolescent line but decreased in middle aged and senile lines. In the present experiments, the duration of the larval stage, and hence longevity, was shorter in offspring produced by old beetles than it was in those produced by recently emerged adults. Ludwig and Barsa (1955) reported that the activity of cytochrome oxidase in the eggs of *T. molitor* is also dependent on parental age, being much higher in eggs laid by recently emerged beetles than in those laid by the same beetles 6 to 8 weeks later. It would be important if a relationship could be established between the activity of this enzyme and the rate of development, longevity, and other known effects of parental age.

SUMMARY

1. Larvae of the mealworm, *Tenebrio molitor*, were reared individually and in groups at the constant temperatures of 25° and 30° C. Determinations were made on the number of molts, and on the duration of each instar on larvae reared individually. Readings were made on the duration of the larval stage of larvae reared in groups.

2. The number of larval molts obtained at 25° varied from 11 to 15, with an average of 13.2. At 30°, it varied from 15 to 23, with an average of 19.1.

3. The duration of each larval instar was shorter at 30° than for the corresponding instars at 25° C. However, because of the greater number of molts which occurred at the higher temperature, the larval period required a longer time.

4. The duration of the larval stage at 30° C. was significantly shorter in larvae reared in groups than it was in larvae reared singly.

5. The duration of the larval stage, and hence longevity, was shorter in offspring produced by old beetles, than it was in those produced by recently emerged adults.

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A CONTRIBUTION TOWARD A MONOGRAPH OF THE SCATOPSIDAE (DIPTERA) PART IV, THE GENUS SWAMMERDAMELLA ENDERLEIN

EDWIN F. COOK[1]

INTRODUCTION

The genus *Swammerdamella* was erected by Enderlein in 1912. The chief characteristics cited in the original description are as follows: the ends of veins R_1 and R_3 are very close together in the costal margin; the cell between veins M_1 and M_2 is very short; the antennae are 12-segmented. The latter is erroneous since only four of the species available to me have as many as 10 antennal segments, and the majority of the species examined have only 9. Neither Duda (1928a) nor Edwards (1930) recognized this as a good genus, and it must be admitted that the characters cited by Enderlein will not always hold. However, on the basis of a fairly adequate collection of North American material and some additional European, Central American and Indian specimens (fourteen species altogether) it seems to be a very sound and distinct group with a wide distribution. The characters that distinguish the genus will be considered in the formal description.

Only four species have heretofore been assigned to this group including the type species, *S. brevicornis* (Mg.), from Europe. These are *S. pygmaea* (Loew) from Washington, D. C., *S. albimana* Edwards (1924, p. 571) from Fiji and *S. approximata* Edwards (1924, p. 571) from Trinidad. Examination of the descriptions and illustrations of Duda (1928a, b) reveals that *Scatopse pediculata* Duda, possibly *Scatopse hungarica* Duda, *Scatopse cingulipes* Strobl. from Europe and *Scatopse aethiopica* Duda from Africa also belong here. In addition, Edwards (1925, p. 271) erroneously synonymized *Scatopse pusilla* Walker with *S. brevicornis* (Mg.). With the exception of *S. brevicornis*, *S. pygmaea* and *S. pusilla*, none of these species have been available to me.

According to the literature *S. brevicornis* is present in North America as well as in Europe; in fact almost all specimens of *Swammerdamella* in American collections are so identified. However, comparison of available North American material with *S. brevicornis* from three areas in England and one in Russia reveals that *S. brevicornis* has not been taken here, and instead we have at least eight distinct North American species in addition to *S. pygmaea* and *S. pusilla*. These will be described as new in this paper. In addition a new north European, a new Indian and a new Central American species will be described.

This genus is represented, then, by five species in Europe, by ten in North America and by one species each in Africa, India, Melanesia, the British West Indies and Central America at the present time. Many more doubtless exist throughout the world.

The immature stages of the species of this genus are unknown and nothing is known of their biology. A single questionable record exists which indicates that some of these may be parasites of phorid pupae (Müller, 1919).

This genus is most closely related to *Rhexoza* considered in the previous paper. The characters shared with *Rhexoza* are as follows: large, laterally flattened, slipper-shaped maxillary palpi (fig. 4–0); one to several setae on the pedicel of the halter; no macrosetae on veins posterior to R_3 nor on the membrane; anterior spiracle set in a narrow, triangular sclerite (fig. 6G).

The characters that serve to distinguish *Swammerdamella* from all other Scatopsidae most readily are as follows: only six abdominal segments are externally visible in the males; male tergum 6 is usually triangularly produced or ornamented and the sternum occasionally so (fig. 4A-F); male segment 7 is always retracted into segment 6; the wings in both sexes (with the exception of *S. pygmaea*) have cell M_1 much

[1]Paper No. 3293, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul 1, Minnesota.

Accepted for publication, Jan. 6, 1955.

shorter than the stem of M, or at most no longer than the stem of M (fig. 3F, G, fig. 4M, fig. 6B, D).

On the basis of adult structure the species of this genus can be divided into five groups. *S. magnifica* from India stands apart from all other members of the genus through the presence of vein R_{4+5}. No other species in the Scatopsinae are known in which this vein is present. The two species *S. pygmaea* and *S. confusa* are also very closely related and distinctive from other North American species in both the structure of the male genitalia and in the presence of ten antennal segments. It seems unusual that two such closely related species should occupy essentially the same very restricted area (Washington. D. C. and vicinity). Because of the small number of specimens and records available no attempt will be made here to interpret this. This will be termed the *Pygmaea* group. The *Marginata* group comprises those species with the posterior margin of the sixth tergum and sternum variously modified (fig. 4D, E, F, fig. 6E). This includes *S. marginata*, *S. sagittata*, *S. nevadensis* and *S. chillcotti*. These species are distributed mostly across southern United States, *S. sagittata* in the east and *S. marginata* in the west. *S. nevadensis* is known from a single specimen from western Nevada and *S. chillcotti* from a single specimen in northern Manitoba. The latter species is also rather similar to the species of the next group which have a more northern distribution. This is the *Brevicornis* group which is quite close to the *Marginata* group in the structure of the male genitalia (fig. 1B, C, G) but differ in having the sixth sternum unmodified. This group includes *S. brevicornis* from Europe and *S. obtusa* and *S. pusilla* Walker from North America. The North American species are widespread, *S. pusilla* ranging in northern Canada from Alaska to the east side of Hudson Bay, north to the Arctic Ocean and south along the Rocky Mountains to Yellowstone National Park. *S. obtusa* is found in southern Canada and in the United States from South Dakota and Kansas to Maine and Maryland. The fifth group is the *Bispinosa* group which includes *S. bispinosa* and *S. reducta* from North America and *S. acuta* from northern Europe. The relationship here is shown in the male genitalic structure (fig. 1H, I, K) and the structure of the seventh segment (fig. 2E, fig. 3A, C). *S. bispinosa* is western in distribution, and *S. reducta* is present in the eastern half of the United States. The only species known from Central America is *S. mojingae* which cannot be placed in any of the above groups.

Swammerdamella Enderlein 1912

Swammerdamella Enderlein, 1912. Zool. Anz. 40: 277–278. Type species: *Scatopse brevicornis* Meigen.

Generic Description

The adults of this genus are all very small in size, varying from 0.86 to 1.90 mm. in total length. The single Indian species is larger, varying from 1.90 to 2.42 mm. in total length. The general coloration is dark grey-brown to black and either dull or feebly shining. The halteres are always dark grey-brown, and the tarsi in most species are concolorous with the rest of the body. The pleural areas of the thorax are usually lighter in color than the scutum and are usually shining.

Head: The head is structurally like that of *Rhexoza* and other genera already considered in this series (fig. 6H). The antennae are 9 to 10-segmented, usually no longer than the head height, of a dull black color and covered with a silvery pubescence. The chaetotaxy is like that of *Rhexoza* except that there may be a few setae on the posterior clypeal margin.

The mouth parts are as in *Rhexoza* with very similar, single-segmented, large maxillary palpi (fig. 4–0). These palpi are flattened laterally and somewhat slipper-shaped in profile.

Thorax: The thorax is well sclerotized and somewhat laterally compressed. Structurally it is very similar to those of the genera already considered (fig. 6F). The sclerite bearing the first spiracle forms an anteroposteriorly elongate triangle as in *Rhexoza* (fig. 6G). There is a well defined row of supra-alar setae in all but one species, and there are from 1 to 7 subspiracular setae. The latter are all small and of a uniform size.

The wings have macrosetae only on the costa, R_1 and R_3. Numerous microtrichia are present on the whole wing surface. Section two of the costal margin is very short, and veins R_1 and R_3 are nearly parallel in most species and terminate well before the middle of the wing. The third section of the costal margin is from 6 to 13 times as long as section two. The branching veins M_1 and M_2 are in almost all species very short while the basal part of the fork is long (figs. 3F, G, 6B, D). M is from 1.75 to 4 times as long as M_1 in all known species with the exception of *S. pygmaea* in which M is equal to or but slightly longer than M^1 (fig. 4M).

The halteres, as in *Rhexoza*, bear one to several setae on the pedicel.

Abdomen: This genus differs from all of the preceding genera in the structure of the male abdomen. There are but six externally visible segments present while the seventh segment is considerably reduced in size and retracted into segment six. In addition, this seventh segment is highly modified in form from that of the typical segment (figs. 2 and 3A, C, E). The tergum is much reduced in size and usually bears one or two median, spine-like, ventrally directed processes. The sternum is larger than the tergum and bears the seventh pair of spiracles. The usual position for these spiracles is in the membrane between the tergum and sternum or

on the tergum itself. It might be assumed that segment seven had rotated through 180 degrees and that the tergum occupies a ventral position. This is apparently not the case in this instance as the genitalia are not rotated and no twisting or distortion of the tracheal trunks is evident. This appears to be unique in this genus.

The female abdomen is like that of the other genera with seven pregenital segments and eight pairs of spiracles. Segment 1 is the shortest in both sexes. Tergum 2 is always a single sclerite. The terga and sterna bear scattered setae and numerous microtrichia. The latter give the sclerites a dull, granular or pollinose appearance in pinned specimens in contrast to the glossy sclerites present in some of the preceding genera. The abdominal membrane is longitudinally ribbed and folded and bears scattered setae. No specialized setae are present.

Male Genitalia (fig. 1A-K, fig. 3B, fig. 6A):

The genitalia are very small in this genus and project but little, if at all, beyond segment 6. They are quite distinctive from any of those previously considered and are all obviously closely related in structure with the exception of those of *S. magnifica* (fig. 3B) and *S. mojingae* (fig. 5K) which are rather distinctive. Homologies are quite obscure, but in most species a single pair of sclerotized, appendage-like processes is present (gonocoxites?) in addition to a pair of short, usually rounded, setaceous lobes (penis valves?). The penis is stoutly sclerotized and short in all but *S. confusa* (fig. 1J). Dorsad of the penis is a sclerotized plate (aedeagal plate) the form of which is distinctive for each species. The genitalia are not rotated. The vesica is free and rather large.

Female Genitalia (fig. 5A-I):

The female genitalia also offer good specific characters in this genus. Tergum 8 is entire in all known species and bears the eighth pair of spiracles. Sternum 8 is either completely divided longitudinally or strongly bilobed.The cerci are quite small in most species and are without macrosetae. Tergum 9 is present as a bilobed sclerite more or less surrounding the cerci. The whole structure is covered with microtrichia. A single, heavily sclerotized, spherical spermatheca is present.

KEY TO THE MALES OF THE KNOWN NORTH AMERICAN SPECIES

1. Antennae 10-segmented 2
1a. Antennae 9-segmented 3
2. M as long as or slightly longer than M_1 (fig. 4M); tergum 7 without a median process; sternum 7 with a truncate median lobe (fig. 2A); genitalia only slightly longer than wide, penis minute (fig. 1A) ..... **pygmaea**
2a. M twice as long as M_1; tergum 7 with a median process; sternum 7 without median lobe (fig. 3E); genitalia elongate, penis larger, half the length of the genitalia (fig. 1J) ..... **confusa**
3. Sternum 6 incised, produced or otherwise ornamented on the posterior margin (fig. 4E, F, D, fig. 6E) 4
3a. Sternum 6 without ornamentation 7
4. Tergum 6 produced posteriorly forming a broad triangle (fig. 6E) ..... **chillcotti**
4a. Tergum 6 otherwise ornamented posteriorly 5
5. Sternum 6 posteriorly sagittate (fig. 4F) ..... **sagittata**
5a. Sternum 6 not so 6
6. Tergum 6 produced posteriorly to form a narrow, truncate lobe; sternum 6 drawn into two, slender, posteriorly projecting processes (fig. 4D) ..... **nevadensis**
6a. Tergum 6 produced into a broad, curved lobe posteriorly; sternum 6 more shallowly incised (fig. 4E) ..... **marginata**
7. Tergum 7 with a slender, apically bifurcate process on the midline in addition to the usual stout median process (fig. 3A); tergum 6 scarcely produced medially ..... **bispinosa**
7a. Tergum 7 with the usual single median process only (fig. 3C, 2C, H); tergum 6 may be produced in a broad triangle posteriorly 8
8. Sternum 7 with a row of small setae posterolaterally on each side (fig. 3C); tergum 6 not produced posteriorly (fig. 4I) ..... **reducta**
8a. Sternum 7 without such seta rows;tergum 6 often posteriorly produced in the form of a triangle 9
9. Male genitalia large, 0.17–0.18 mm. long (fig. 1G); large species with wing length of 1.13–1.38 mm. ..... **pusilla**
9a. Male genitalia small, 0.08–0.10 mm. long (fig. 1C); smaller species with wing length of 0.69–0.96 mm. ..... **obtusa**

KEY TO THE KNOWN FEMALES OF THE NORTH AMERICAN SPECIES

The females of *S. confusa*, *S. nevadensis*, *S. reducta* and *S. chillcotti* are unknown.

1. Antennae 10-segmented ..... **pygmaea**
1a. Antennae 9-segmented 2
2. Tergum 8 produced posteriorly at lateral margins, medially emarginate (fig. 5B) ..... **sagittata**
2a. Tergum 8 never produced posteriorly at sides 3
3. Sternum 8 with a wide, median, inverted V-shaped incision (fig. 5D) ..... **bispinosa**
3a. Sternum 8 with a narrow, median incision (fig. 5E, F, H) 4
4. Tergum 8 with a delicate, broad extension of the posterior margin covering most of the cerci (fig. 5H) ..... **marginata**
4a. Tergum 8 without such an extension 5
5. Tergum 8 with a single row of setae; each lateral lobe of sternum 8 bilobed (fig. 5F) ..... **obtusa**
5a. Tergum 8 with several irregular rows of setae; each lateral lobe of sternum 8 entire (fig. 5E) ..... **pusilla**

Swammerdamella brevicornis (Meigen)

Scatopse brevicornis Meigen, 1830. Syst. Besch. VI: 314.
Swammardamella brevicornis (Mg.). Enderlein, 1912, Zool. Anz. 40: 277–278.
Scatopse brevicornis Meigen. Duda, 1928, *in* Lindner, Die Fliegen der Palaearktischen Region, II, Fasc. 5, pp. 15–16.
[non] *Swammerdamella brevicornis* (Mg.). Melander, 1916, State Coll. Wash. Ag. Exp. Sta. Bull. 130, pp. 8–9.
[non] *Swammerdamella brevicornis* (Mg.). McAtee. 1921, Proc. Ent. Soc. Washington 23: 122.

A more complete list of citations up to 1927 is available in Duda (1928a). This species has been described extensively by Duda, and the wing venation has been illustrated, as have the male genitalia (from pinned specimens). Only a very few specimens of this species have been

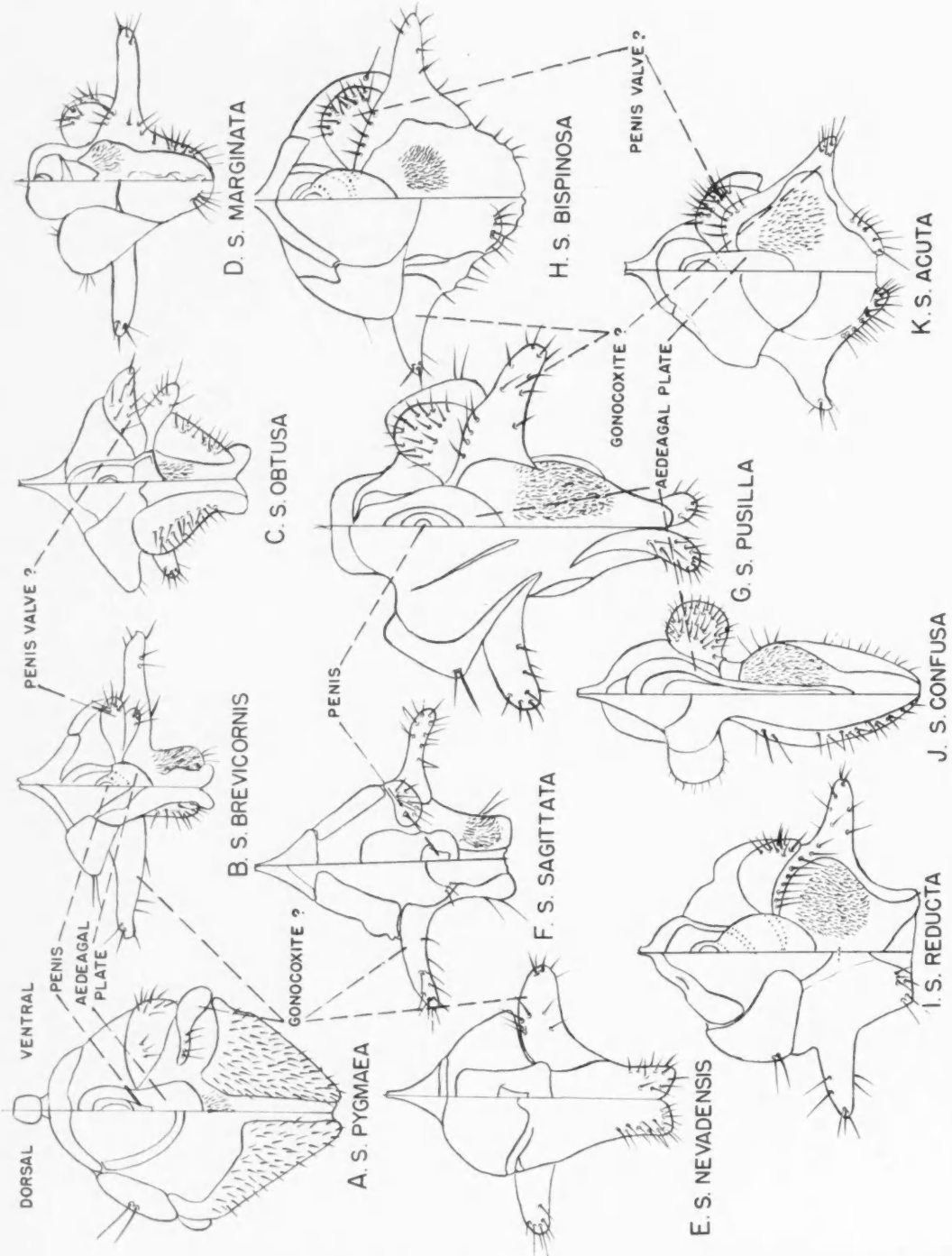

FIG. 1. Male genitalia of *Swammerdamella*.

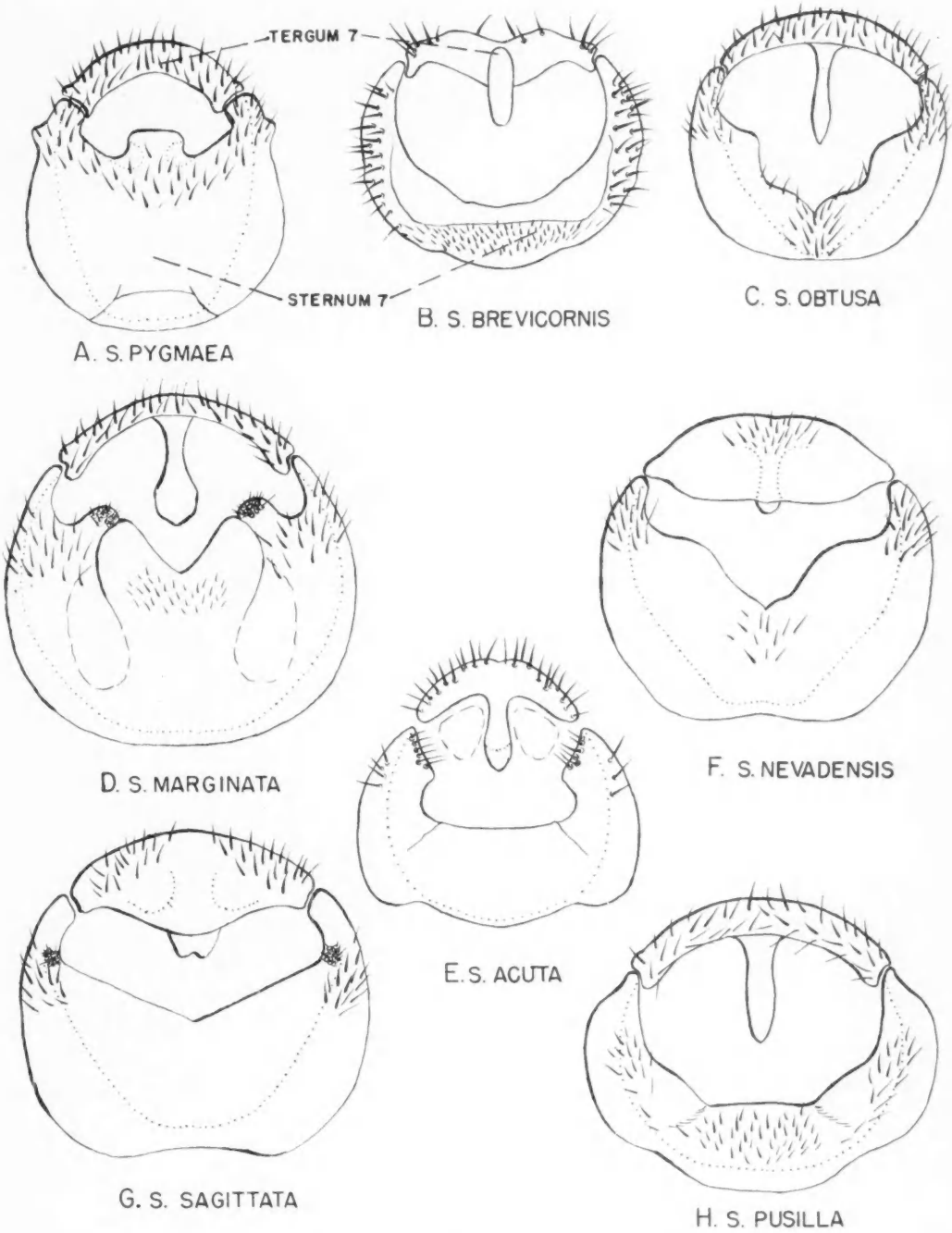

FIG. 2. Seventh segments of male *Swammerdamella* spp.

available to me, but they will be described here in order to include characters found to be essential to this study.

Male. Total length 1.00–1.50 mm. long (*fide* Duda, 1928a). Color very dark grey-brown, feebly shining on head and thorax, otherwise dull; tarsi concolorous with rest of body; setae on abdomen, legs and antennae silvery. Antennae 9-segmented; maxillary palpi 0.12 mm. long; enlarged supra-alar setae present in a definite row, 10 in number; 6 small subspiracular setae present.

Wings 1.03 mm. long; section 3 of costal margin 7.25 times as long as section 2; M 3.00 times as long as M_1 (fig. 6D).

Tergum 6 of abdomen forming a broad triangle posteriorly, bilobed anteriorly (fig. 4A). Segment 7 not particularly modified, tergum narrow with a large median spine-like process, sternum with posterior margin forming a smooth semicircle (fig. 2B). Genital vesica and apodemes 0.14 mm. long. Genitalia (fig. 1B) relatively short and broad, with gonocoxites long and penis valves bilobed, each lobe bearing setae; aedeagal plate semi-elliptical.

Females: Total length 1.55–1.80 mm.; wing length 1.28–1.34 mm. Supra-alar setae 13; subspiraculars 7. Otherwise as male in color and chaetotaxy.

Genitalia (fig. 5A) with tergum 8 bearing numerous setae on posterior half; cerci small, partially covered by a thin posterior extension of tergum 8. Sternum 8 completely divided longitudinally, with a single row of setae at posterior margins.

Comments: This species has a wide distribution in Europe according to the literature, but it apparently does not occur in North America. Some northern European records (Frey, 1931) might also be open to question since a very distinctive new species has been discovered in material from Sweden and Scotland.

Specimens examined: 1♂, Essex, Brentwood, England, July 29, 1947; 1♂, Philipoffka, Samara, Russia, Aug. 28, 1927; 4♀ ♀, Ditchling Common, Sussex, England, Aug. 3, 1951.

Swammerdamella acuta n. sp.

Males: Total length 1.00–1.20 mm. Color very dark grey-brown, entirely subshining; head and scutum jet black; antennae 9-segmented, dull black with silvery pubescence; setae brown; tarsi concolorous with body. Maxillary palpi 0.08 mm. long. Enlarged supra-alar setae in a definite row, 15 or 16 in number; subspiraculars 1 to 3.

Wings 1.00–1.24 mm. long; section 3 of costal margin 10 to 13 times as long as section 2; vein M three times as long as M_1.

Tergum 6 of abdomen forming a rather narrow acute triangle posteriorly, slightly bilobed anteriorly (fig. 4K). Segment 7 with fewer setae than in *S. brevicornis;* tergum 7 narrow with a stout median spine. Sternum 7 with a few setae on each side and with distinct rows of small setae on each side at posterior margin (fig. 2E). Genital vesica and apodemes much longer than in *S. brevicornis,* 0.25 mm. long. Genitalia (fig. 1K) with gonocoxites short; penis valves not bilobed; aedeagal plate oblong and apically rounded.

Females: Total length 1.00+mm. (slide mounted specimen). Wing length 1.05 mm. Supra-alar setae 15; subspiraculars 4. Otherwise as males in color and chaetotaxy.

Genitalia (fig. 5G) with tergum 8 bearing but a few setae in a single row; no posterior extension of tergum 8, but small cerci articulate beneath the posterior margin. Sternum 8 completely divided longitudinally with a single seta on the posterior margin of each lobe.

Comments: This is a northern European species, specimens of which have been available from Scotland and Sweden. It is most closely related anatomically to the North American species *S. bispinosa* and *S. reducta.*

Specimens examined:

Holotype: ♂, Pajala Nb. Sweden, July 27, 1951, J. R. Vockeroth. Allotype: ♀, same data. Types in the Canadian National Collections. Paratypes: 6♂ ♂, same data as above; 1♂, Bonhill, Dumbartonshire, Scotland, July, 1912.

Swammerdamella magnifica n. sp.

Males: Total length 1.90–2.24 mm. Color dark grey-brown; pronotum and sides of thorax paler, with a reddish cast; head jet black, dull; scutum and pleural areas somewhat shining; antennae dull black; tarsi pale yellowish brown; wings pale brown, densely covered with long microtrichia. Antennae 10-segmented. Maxillary palpi 0.15 mm. long, very wide basally. Enlarged supra-alar setae in a definite row, 12 to 17 in number; subspiraculars 1.

Wings (fig. 3F) 2.00–2.22 mm. long. These are unusual in that a very faint vein (R_{4+5}) continues from near the apex of R_3 and the end of the costa nearly to the apex of M_1. Section 3 of costal margin 7.5 times as long as section 2; M_2 incomplete basally, consequently the length of M_1 relative to M cannot be determined.

Tergum 6 of abdomen somewhat bilobed basally and apically (fig. 4L); sternum 6 simple and unmodified. Segment 7 with tergum small, a short, stout, apically emarginate median process; sternum 7 simple, with a few setae on each side and medially (fig. 3D). Genital vesica and apodemes 0.34–0.37 mm. long. Genitalia (fig. 3B) with gonocoxites directed posteriorly rather than laterally; penis valves apparently absent; aedeagal plate short, broad and truncate.

Females: Total length 2.00–2.42 mm.; wing length 2.10–2.52 mm. Antennae sometimes pale yellowish grey (possibly teneral specimens); female genitalia paler than abdomen. Supra-alar

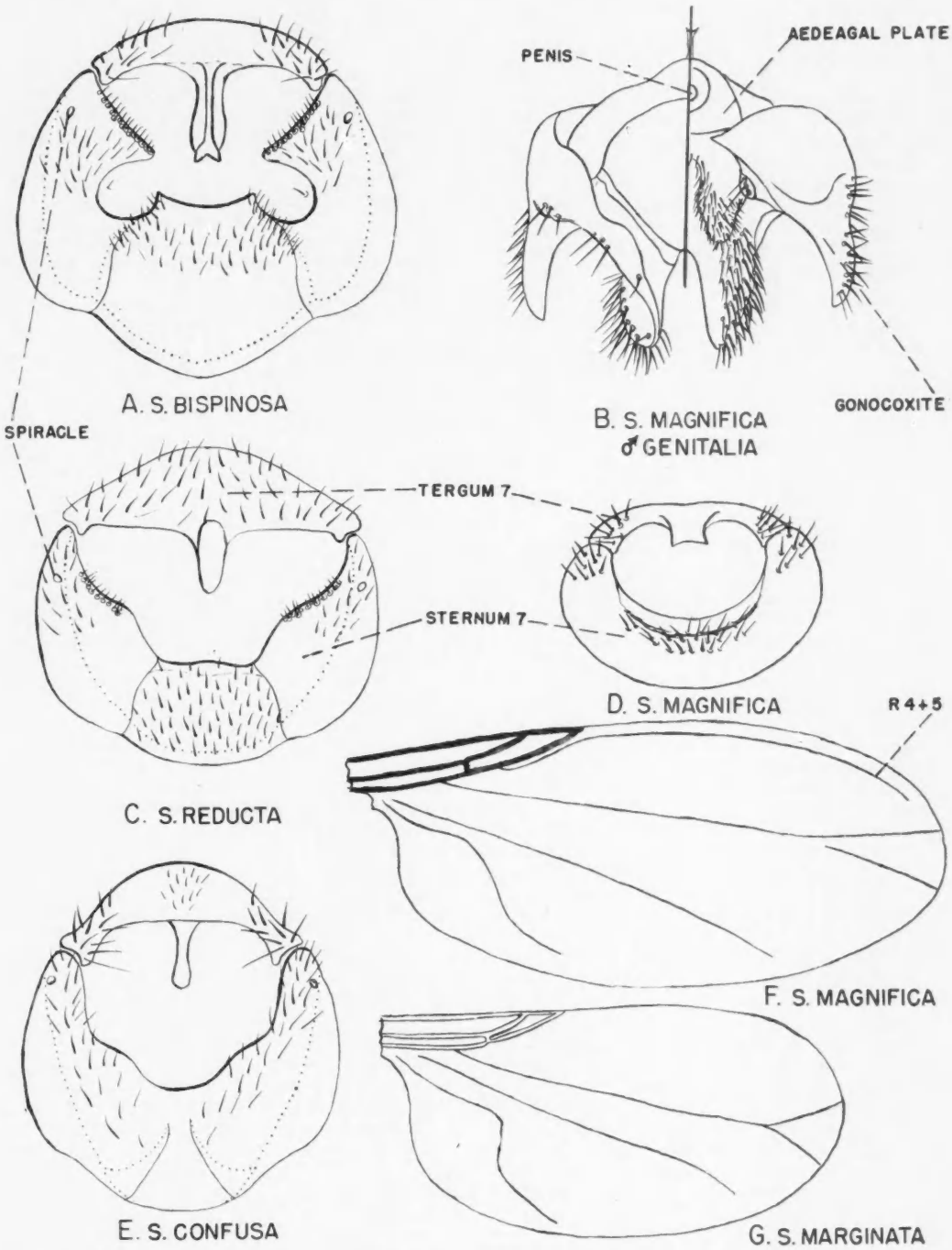

FIG. 3. A, C, D and E, Seventh segments of *Swammermadella* spp.; B, male genitalia of *S. magnifica;* F and G, wings.

setae 13 or 14; subspiraculars 1. Otherwise as male in color and chaetotaxy.

Genitalia (fig. 5I) with tergum 8 bare of macrosetae but with numerous rather long microtrichia; cerci minute; sternum 8 almost completely divided longitudinally, a very few setae on posterior margin of each lobe.

Comments: The wing venation sets this species apart from all other members of the genus known at the present time. That it does belong in this genus is evident, however, from the form and structure of segments 6 and 7 in the males and the structure of the female genitalia.

Specimens examined:

Holotype: ♂, Nilgiri Hills, S. India, Dedabetta, July, 1950, P. S. Nathan. Allotype: ♀, same data. Types in the Canadian National Collections. Paratypes: 7♂♂, 8♀♀, same data.

Swammerdamella pygmaea (Loew)

Scatopse pygmaea Loew, 1864. Berlin Ent. Zeit. 8: 56, Cent. V, No. 13.
Rhegmoclema floralis McAtee, 1921. Proc. Ent. Soc. Washington 23: 123–124. *New synonymy.*
[non] *Scatopse pygmaea* Loew. Williston, 1896, Trans. Ent. Soc. London, 1896: 269, Pl. VIII, Fig. 26[2].

Males: Total length between 1.00 and 1.50 mm. (slide mounts). Color dark grey-brown, head and thorax feebly shining, remainder dull; tarsi paler, yellowish; setae brown. Maxillary palpi .12–.13 mm. long. Antennae 10-segmented. Enlarged supra-alar setae in a definite row, 8–10 in number; 1–2 small subspiraculars.

Wings 1.17–1.24 mm. long. Section 3 of costal margin 6 times as long as section 2; vein M as long as or slightly longer than M_1.

Tergum 6 of abdomen large, broadly rounded laterally, bilobed anteriorly, broadly triangular posteriorly (fig. 4B); sternum unmodified. Segment 7 without a median spine-like process at midline of tergum; sternum shallowly emarginate, with a short, truncate median lobe (fig. 2A). Genital vesica and apodemes 0.22–0.24 mm. long. Genitalia (fig. 1A) with posterior lobes much enlarged; gonocoxites very small and penis valves large; aedeagal plate spatulate, apically rounded; penis short.

Females: Total length 1.38–1.48 mm. Wing length 1.20–1.38 mm. Supra-alar setae 9 to 13; subspiraculars 1. Otherwise as male in color and chaetotaxy.

Genitalia (fig. 5C) without macrosetae on tergum 8, although numerous, rather long microtrichia are present; cerci somewhat triangular in form, some specimens with 1 or 2 macrosetae; sternum 8 bilobed but not completely divided.

[2]Williston's species has been renamed *Rhegmoclema willistoni* by McAtee (*ibid.* p. 124). This species is undoubtedly a *Rhegmoclemina* but cannot be definitely determined unless the specimen is still extant in the British Museum.

Comments: This species is widely divergent from all other species of the genus with the exception of *S. confusa* n.sp. in the possession of 10 antennal segments, in the structure of the male and female genitalia and in the long M fork.

The distribution is seemingly remarkably restricted as may be determined from the list of specimens examined.

Dr. P. J. Darlington, Jr. of Harvard University very kindly compared my sketch of the wing of a paratype of *R. floralis* McAtee with the wing of the holotype of *S. pygmaea* (Loew) in the Museum of Comparative Zoology and provided comparative measurements of the wing veins. The responsibility for this synonymy is the author's.

Specimens examined: One♂, 1♀ (paratypes of *R. floralis*), Plummers Island, Maryland, April 28, 1915, at flowers of *Staphylea trifoliata;* 1♂, 1♀, Cabin John Bridge, Maryland, April 28, 1912; 1♀, Plummers Island, July 1, 1903; 1♀, Rock Creek Park, Washington, D. C., May 28, 1922; 1♀, Plummers Island, May 10, 1914, under bark of honey locust.

Swammerdamella confusa n. sp.

Males: Total length 1.13–1.38 mm. Color dark grey-brown, sides of thorax feebly shining, remainder of body dull; tarsi pale yellowish brown; antennae 10-segmented, dull black and covered with silvery pubescence; wings slightly infuscated; setae of abdomen and legs silvery, remaining setae brown or black. Maxillary palpi 0.12 mm. long; enlarged supra-alar setae in a definite row, 11 or 12 present; subspiraculars 2.

Wings 1.00–1.07 mm. long; section 3 of costal margin 6.5 times as long as section 2; vein M twice as long as M_1. The point of branching of M_1 and M_2 from M often obscure.

Tergum 6 of abdomen large, parallel sided, strongly bilobed anteriorly, acutely triangular posteriorly (fig. 4J); sternum 6 without distinguishing characteristics. Segment 7 with a median, spine-like process on tergum; sternum deeply and sinuously emarginate posteriorly, without a median lobe (fig. 3E). Genital vesica and apodemes 0.22–0.24 mm. long. Genitalia (fig. 1J) elongate and narrow; posterior lobes large; gonocoxites apparently absent; penis valves rounded, setaceous lobes; aedeagal plate long, lanceolate; penis long.

Females: Unknown.

Comments: This species is very closely related to *S. pygmaea*. These two are the only known North American species with 10 antennal segments. In addition, these species are much alike in many other features such as color and chaetotaxy. The differences in the structure of abdominal segment 7 and the male genitalia are, however, very clear.

This species is known only from three specimens collected in Virginia.

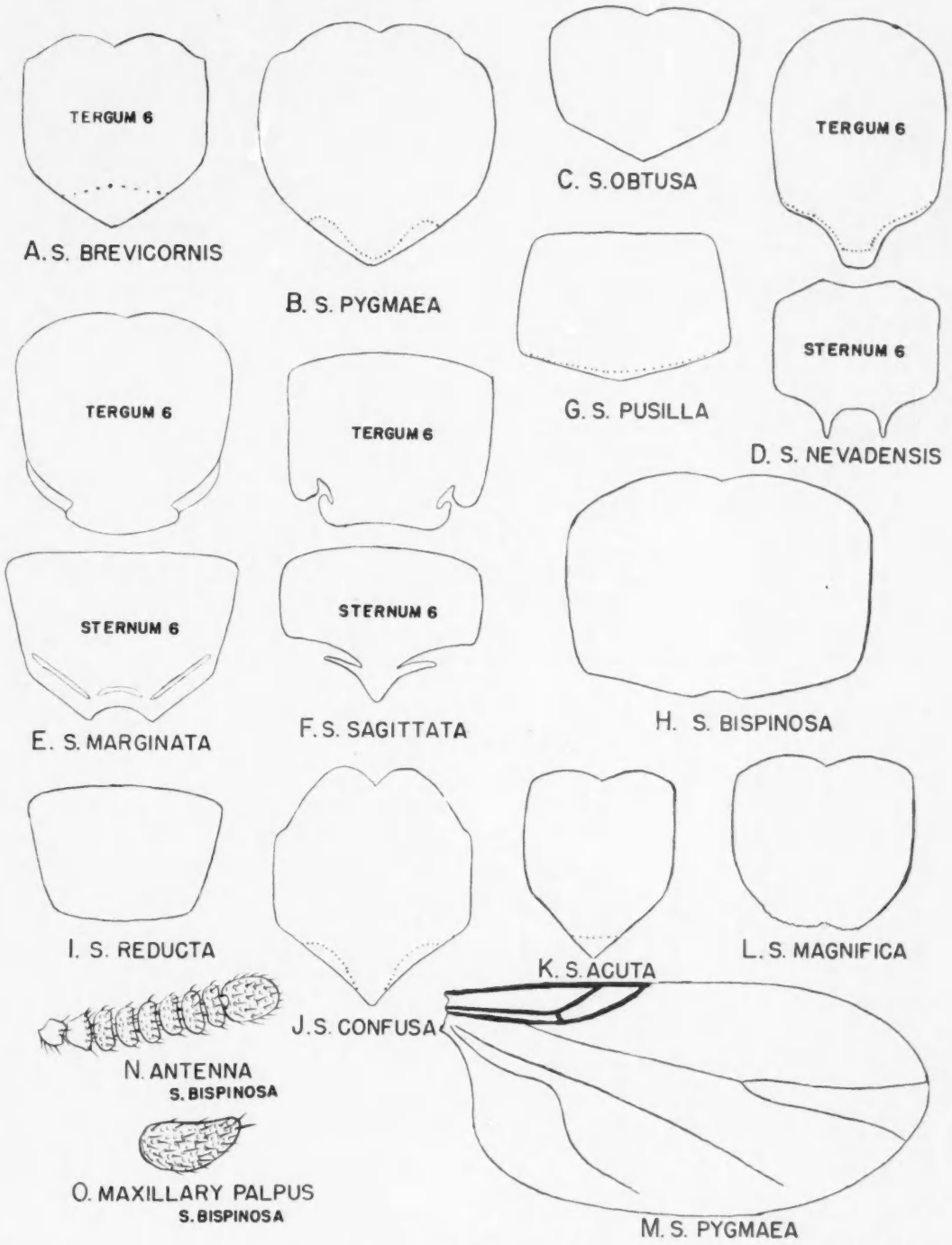

FIG. 4. A–L, Segment 6 of males; M, wing of *S. pygmaea;* N. antenna of *S. bispinosa;* O, maxillary palpus of *S. bispinosa.*

Specimens Examined:

Holotype: ♂, Maywood, Alexandria Co., Virginia, July 3, 1922, W. L. McAtee. Type in the U. S. National Museum. Paratypes: 1♂, Maywood, Alexandria Co., July 2, 1922; 1♂, Mt. Solon, Augusta Co., Virginia, July 11, 1950, stream margin.

Swammerdamella marginata n. sp.

Males. Total length 1.30–1.38 mm. Color dark grey-brown; head and abdomen jet black, feebly shining; setae silvery except for supra-alars and scutellars; tarsi paler owing to dense silvery pubescence. Antennae 9-segmented; maxillary palpi 0.11–0.12 mm. long. Supra-alar setae 15 or 16, in a definite row; subspiraculars 3–5.

Wings 1.06–1.20 mm. long; section 3 of costal margin eight to nine times as long as section 2; vein M 2.5 to 3.0 times as long as M_1.

Tergum and sternum 6 both modified on posterior margin; tergum 6 with a broad, rounded medial lobe; sternum 6 medially emarginate (fig. 4E). Segment 7 with a single apically enlarged, medial spine on tergum; sternum with an angulate medial and rounded lateral emarginations on posterior margin, a cluster of minute setae in middle of posterior margin on each side (fig. 2D). Genital vesica and apodemes 0.30–0.36 mm. long, larger than in preceding species. Genitalia (fig. 1D) rather short and chordate; gonocoxites long and slender; penis valves rounded; aedeagal plate apically incised.

Females: Total length 1.45–1.83 mm.; wing length 1.20–1.45 mm. Supra-alar setae 15–17; subspiraculars 1–5. Otherwise as males in color and chaetotaxy.

Genitalia (fig. 5H) with tergum 8 bearing a single, sparse row of setae; a thin, transparent, posterior extension of tergum also bears a single row of setae; the latter extension almost conceals rather large cerci; sternum 8 bilobed but not entirely divided.

Comments: The distribution of this species is primarily southwestern with specimens recorded from central Mexico to central California and Nevada.

Specimens examined:

Holotype: ♂, Las Vegas H. S., New Mexico, Mar. 8, H. S. Barber. Allotype: ♀, same data. Types in U. S. National Museum Collections.

Paratypes: *California:* 1♂, 1♀, Upland, San Bernardino Co., May 16, 1950, Citronella bait trap; 1♂, 1♀, Davis, June 22, 1936; 1♀, Oct. 27, 1952; 1♀, Temacula, Riverside Co., April 24, 1951; 1♀, Los Angeles Co., March; 1♂, Riverside, Nov. 29, 1934; 1♀, Mar. 10, 1935; 1♀, Upper Santa Ana River, Aug. 28, 1947; 1♀, Buena Park, Dec. 23, 1944; 1♂, 1♀, Redwood City, May 15, 1954; *Nevada:* 1♀, Reno, Aug. 31, 1915; *Mexico:* 1♂, 2♀♀, Guadalajara, July 7, 1913.

Swammerdamella sagittata n. sp.

Males: Total length 1.10–1.31 mm. Color dark grey-brown; head and disc of scutum black; head and thorax feebly shining, abdomen dull, pollinose; tarsi, especially metathoracic tarsi, pale yellowish grey; setae pale brown or silvery except supra-alar row and scutellars black. Antennae 9-segmented; maxillary palpi 0.10–0.12 mm. long. Supra-alar setae 12 to 17, in a definite row; subspiraculars 1 or 2.

Wings 0.96–1.10 mm. long; section 3 of costal margin 7.0 to 8.5 times as long as section 2; vein M 3.0 to 3.5 times as long as M_1.

Tergum and sternum 6 of abdomen both modified on posterior margin; tergum 6 with a broad, slightly emarginate median lobe posteriorly, anterior margin not bilobed; sternum with a sagittate median process on the posterior margin (fig. 4F). Segment 7 (fig. 2G) with a short, stout median spine on tergum, tergum wider than in *S. marginata*; sternum 7 with an angular posterior emargination, a cluster of minute setae at posterior margin on each side, no mesal setae. Genital vesica and apodemes 0.22–0.25 mm. long, shorter than in *S. marginata*. Genitalia (fig. 1F) small; gonocoxites rather long and slender; penis valves quite small and not projecting laterally; aedeagal plate short, rounded anteriorly; penis small.

Females: Total length 1.03–1.45 mm.; wing length 0.96–1.27 mm.; supra-alar setae 13 or 14; subspiraculars 1 or 2. Otherwise as males in color and chaetotaxy.

Genitalia (fig. 5B) with tergum 8 bearing numerous setae on posterior half; posterior margin of tergum emarginate; cerci large and almost entirely exposed; sternum 8 bilobed, with a number of setae on posterior margin of each lobe.

Comments: This species is a member of the *Marginata* group as evidenced by the structure of segments 6 and 7 in the males and the male and female genitalia. It is apparently distributed largely in southeastern United States, ranging from Texas to Florida and north to Pennsylvania and Virginia.

Specimens examined:

Holotype: ♂, Kirbyville, Texas, Mar. 20, 1908, E. S. Tucker, on *Lonicera*. Allotype: ♀, Denton, Texas, Sept. 12, 1906. Types in the U. S. National Museum. Paratypes: *Florida:* 1♀, St. Petersburg, Mar. 30, 1932; *Georgia:* 1♀, Waycross, May 8, 1911; 2♂♂, 2♀♀, St. Simon Island, April 22—May 12, 1911; *Illinois:* 1♂, 3♀♀, Dongola, May 9–12, 1916; *Pennsylvania:* 1♂, Pittsburg, May 20, 1907, on window; 1♂, Oct. 4, 1907; *Texas:* 1♀, Denton, Sept. 12, 1906; 1♀, San Antonio, April 11, 1942; *Virginia:* 2♂♂, Alexandria, April 11, 1952.

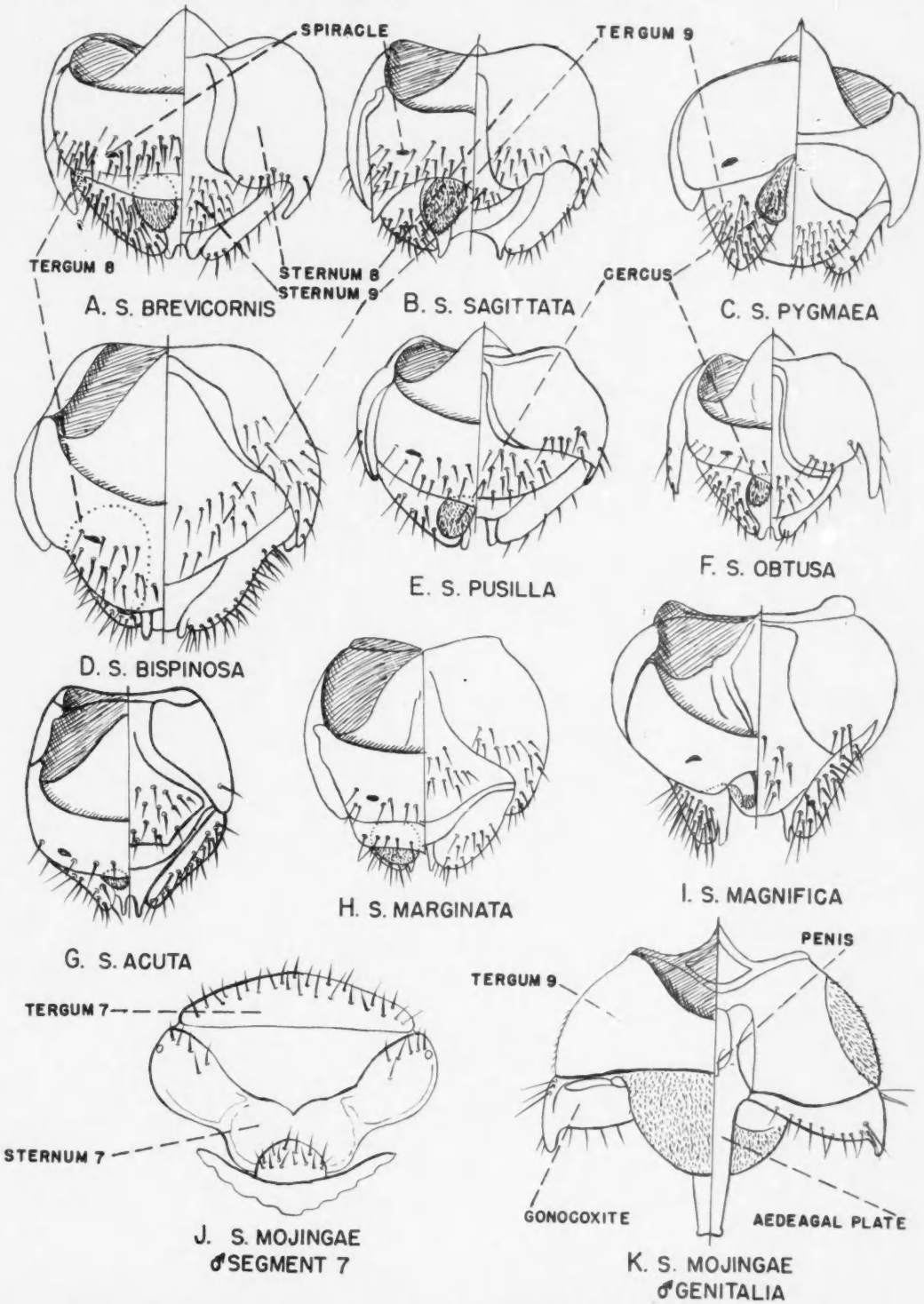

FIG. 5. A–I, female genitalia; J, segment 7 of male *S. mojingae;* K, male genitalia of *S. mojingae.*

Swammerdamella nevadensis n. sp.

Male: Total length 1.00 +mm. (slide mounted specimen). Color dark grey-brown, feebly shining; head somewhat darker; tarsi slightly paler than general body color; setae pale except for supra-alar and scutellars. Antennae 9-segmented; maxillary palpi 0.12 mm. long. Supra-alar setae 12, in a definite row; 1 subspiracular.

Wings 0.97 mm. long; section 3 of costal margin nine times as long as section 2; vein M 3.5 times as long as M_1.

Tergum and sternum of abdominal segment 6 (fig. 4D) modified on posterior margin; tergum 6 with a rather narrow, truncate median lobe, anteriorly arcuate but not bilobed; sternum 6 prolonged posteriorly in two spine-like processes. Segment 7 (fig. 2F) with a rather broad tergum bearing the usual median process; sternum 7 shallowly and sinuously emarginate posteriorly, no cluster of minute setae at posterior margin. Genital vesica and apodemes 0.22 mm. long, smaller than in *S. marginata*. Genitalia (fig. 1E) rather small, similar to those of *S. marginata;* gonocoxites shorter and stouter; penis valves without setae; aedeagal plate apically spatulate; penis small.

Females: Unknown.

Comments: This species is also clearly in the *Marginata* group but is quite readily distinguished from *S. marginata* by the characters given in the key and also by the male genitalia and the size of the genital vesica and apodemes.

Specimen examined:

Holotype: ♂, Steamboat, Nevada, May 13, 1917, H. G. Dyar. Type in the U. S. National Museum.

Swammerdamella chillcotti n. sp.

Male: Total length 1.00+ mm. (slide mounted specimen). Color very dark grey-brown, thorax somewhat shining at sides, otherwise dull; tarsi concolorous with body. Antennae 9-segmented; maxillary palpi 0.07 mm. long. Supra-alar setae 9, in a definite row; 1 subspiracular.

Wings 0.83 mm. long; section 3 of costal margin 8.5 times as long as section 2; vein M three times as long as M_1.

Tergum 6 (fig. 6E) of abdomen produced to an obtuse angle posteriorly, slightly lobed at each side of the angulate projection; bilobed on anterior margin. Sternum 6 deeply emarginate posteriorly (fig. 6E). Segment 7 (fig. 6C) with tergum much larger than in preceding species, the usual median process present; sternum without paired clusters of minute setae, a few setae medially and laterally. Genital vesica and apodemes 0.13 mm. long, much smaller than in any other member of the *Marginata* group. Genitalia (fig. 6A) short and broad; gonocoxites short, acute apically, broad basally; penis valves lobed; aedeagal plate very broad, apically serrate; penis small.

Females: Unknown.

Comments: This species shares characters with the *Marginata* group (structure of sternum 6 and segment 7) and also with the *Brevicornis* group (short vesica, structure of male genitalia) described below. It thus forms an intermediate between these larger groups.

Specimen examined:

Holotype: ♂, Farnsworth Lake, nr. Churchill, Manitoba, June 12, 1952, J. G. Chillcott. Type in the Canadian National Collections.

Swammerdamella obtusa n. sp.

Males: Total length 0.93–1.20 mm. Color dark grey-brown to nearly jet black, feebly shining; setae silvery; tarsi somewhat paler, sometimes yellowish, especially metathoracic tarsi. Antennae with nine segments, maxillary palpi 0.10–0.12 mm. long. Supra-alar setae 11 to 16, in a definite row; 1 to 6 subspiraculars.

Wings 0.69–0.96 mm. long; section 3 of costal margin 7.5 to 9.5 times as long as section 2; vein M 3.0 to 3.5 times as long as M_1.

Tergum 6 (fig. 4C) of abdomen drawn into an obtuse triangle posteriorly, bilobed anteriorly; sternum 6 without notable modification. Segment 7 (fig. 2C) of abdomen with tergum rather narrow, bearing a large, median, spine-like process; sternum large, posterior margin sinuously incised, no specialized groups of setae. Genital vesica and apodemes 0.12–0.16 mm. long. Genitalia (fig. 1C) small; gonocoxites short and stout; penis valves larger than gonocoxites, with a pointed apex; aedeagal plate short, apically triangular; penis short.

Females: Total length 1.04—1.48 mm.; wing length 0.93–1.20 mm. Supra-alar setae 12 to 20; subspiraculars 2 or 3. Otherwise as males in color and chaetotaxy, except tarsi rarely paler than other leg segments.

Genitalia (fig. 5F) with tergum 8 bearing a single, rather sparse row of setae; cerci small, basally concealed by posterior margin of tergum; sternum 8 bilobed but not completely divided; both major lobes also bilobed, a few setae at posterior margins.

Comments: This species is rather closely related to *S. pusilla* (Walker), the description of which follows, as evidenced by the form of tergum 6 and segment 7 in the males. There is also some relationship between this species and *S. chillcotti* in the structure of the male genitalia and in the size of the genital vesica.

This is apparently the most abundant and widespread North American species. Its range extends from Saskatchewan to Ontario in the north to Kansas and Washington, D. C. in the south.

Specimens examined:

Holotype: ♂, University Farm, St. Paul, Minn., June 29, 1954, M. E. Warters. Allotype:

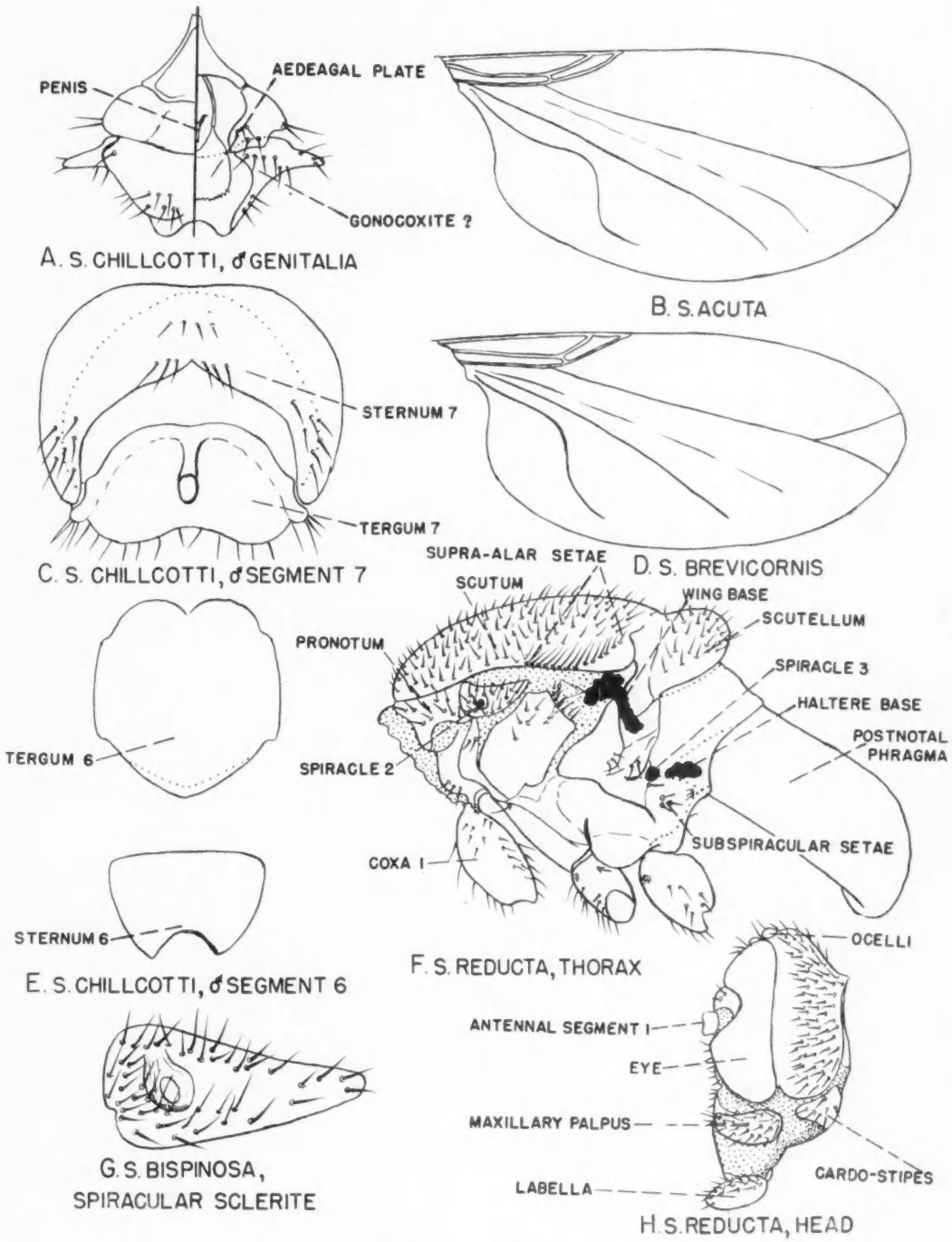

FIG. 6. Miscellaneous structures of *Swammerdamella*

♀, same data. Types in the University of Minnesota Collections. Paratypes: 1♂, 1♀, same data as above (slide mounts); 12♂♂, 7♀♀, same data as above (alcoholic specimens). Other specimens examined: 68♂♂, 71♀♀ from: *Illinois:* Robertson, Urbana, White Heath, Grand Tower, Algonquin, May 14 to July 21; *Indiana:* LaFayette, May 7 to Aug. 8; *Iowa:* Ames, Ankeny, Sioux City, May 3 to July 28; *Kansas:* Lawrence, July 2; *Maine:* Kennebunkport, August; *Maryland:* Beltsville, July 24; *Minnesota:* Ramsey Co., University Farm, St. Paul, Cass Co., Cook Co., Itasca State Park, May 21 to Aug. 21; *Missouri:* Columbia, May 26 to June 8; *Nebraska:* 30 mi. S. of Valentine, June 9; *New Hampshire:* Mt. Washington, Aug. 13; *New York:* Ithaca, Lake Placid, May 11 to July 29; *Ontario:* Ottawa, Marmora, S. March, Vineland Sta., May 3 to Oct. 5; *Pennsylvania:* Pittsburg, May 17 to July 27; *Quebec:* Laniel, June 21; *Saskatchewan:* Saskatoon, White Fox, Indian Head, June 17 to Aug. 11; *South Dakota:* Erwin, Winner, June 4 to July 3; *Washington, D. C.*, June 6 to Oct. 3.

Swammerdamella pusilla (Walker)

Scatopse pusilla Walker, 1848. List of the Specimens of Dipterous Insects in the British Museum, Part I, p. 114.
[non] *Swammerdamella brevicornis* (Mg.). Edwards, (in part), 1925, Ann. of Applied Biol. 12: 271.
Type locality, St. Martins Falls, Albany River, Canada. Types (2♀♀) in the British Museum (Natural History).

Males: Total length 1.03–1.62 mm. Color dark grey-brown to nearly jet black; head and thorax darker, feebly shining, abdomen dull; setae golden to silvery; silvery setae on antennae, tibiae and tarsi make these seem paler, ground color of tarsi concolorous with rest of body. Antennae 9-segmented; maxillary palpi 0.10–0.12 mm. long. Supra-alar setae 12 to 17, in a definite row; 2 to 7 small subspiraculars.

Wings 1.13–1.38 mm. long; section 3 of costal margin 7.5–8.5 times as long as section 2; vein M 3.0 to 3.5 times as long as M_1.

Tergum 6 (fig. 4G) with anterior margin not bilobed, posterior margin drawn into a broad, obtuse triangle, sometimes more acute than in illustration; sternum unmodified. Segment 7 (fig. 2H) with tergum narrow, bearing a large median spine; sternum with median and lateral setae. Genital vesica and apodemes 0.22–0.27 mm. long. Genitalia (fig. 1G) large; gonocoxites stout; penis valves rounded; aedeagal plate semi-elliptical; penis small.

Females: Total length 1.28–1.65 mm.; wing length 1.13–1.45 mm; 15 to 18 supra-alar setae; 4 or 5 subspiraculars. Otherwise identical with male in color and chaetotaxy.

Genitalia (fig. 5E) much like those of *S. obtusa* except tergum 8 bears more numerous setae, and each lobe of sternum 8 is entire.

Comments: This is a widespread arctic form which seems to replace *S. obtusa* in the north as our most common species. It is distributed from Alaska to the eastern side of Hudson Bay, from the Mackenzie Delta to Saskatoon, Saskatchewan. It also enters the United States along the Rocky Mountains where it has been taken as far south as Yellowstone National Park.

Dr. Paul Freeman of the British Museum very kindly compared specimens with the types and indicated (*in litt.*) that the above described species is similar in size and in the anatomy of the female genitalia. The author assumes responsibility for the determination, however.

Specimens examined:

Alaska: 4♂♂, Anchorage, June 16, 1921; 1♀, Circle, June 25, 1948; *Alberta:* 1♂, Lethbridge, June 26, 1923, clover blossom; *Manitoba:* 2♂♂, 6♀♀, Churchill, Aug. 2–9, 1937; 1♂, June 25, 1947; 1♀, June 26, 1952; 1♂, 1♀ (in copula), Eastern Cr. nr. Churchill, July 9, 1952; *Northwest Territories:* 2♂♂, 1♀, Reindeer Depot, Mackenzie Delta, June 28–Aug. 17, 1948; *Quebec:* 4♂♂, 2♀♀ (one bred from *Microtus* nest), Great Whale River, June 26–Aug. 15, 1949; *Saskatchewan:* 1♂, Saskatoon, July 9, 1935; *Wyoming:* 5♂♂, Yellowstone National Park, Aug. 4–19, 1918.

Swammerdamella bispinosa n. sp.

Males: Total length 1.52–1.72 mm. Color dark grey-brown; head and thorax feebly shining, abdomen dull; setae brown, except supra-alars and scutellars black; tibiae and tarsi of middle and hing legs lighter brown. Antennae dull black with silvery setae, nine segments; maxillary palpi 0.14 mm. long. Supra-alar setae 15 to 17, in definite row; 2 to 4 subspiraculars, uniform in size but larger than in preceding species.

Wings 1.40–1.62 mm. long; section 3 of costal margin 7.0 to 8.5 times as long as section 2; vein M three times as long as M_1 (the point of branching of M_1 and M_2 is sometimes obscure).

Tergum 6 (fig. 4H) only slightly if at all produced posteriorly, somewhat bilobed anteriorly; sternum 6 unmodified. Segment 7 (fig. 3A) with a slender, apically bifurcate, spinose process in addition to the usual median process on the tergum; sternum 7 with a complex posterior emargination, a row of small setae on the posterior margin laterally and a number of setae medially and laterally. Genital vesica and apodemes 0.43–0.44 mm. long (much larger than in any of the previously described species). Genitalia (fig. 1H) rather large, somewhat wider than long; gonocoxites stout, well sclerotized; penis valves small, rounded; aedeagal plate ovate; penis small.

Females: Total length 1.38–1.72 mm.; wing length 1.38–1.62 mm.; supra-alar setae 18 to 20; subspiraculars 4. Otherwise as males in color and chaetotaxy.

Genitalia (fig. 5D) quite distinctive from those of all other species seen. Tergum 8 large, produced posteriorly in a rounded lobe entirely concealing the very large cerci. Sternum 8 very broadly and deeply emarginate posteriorly.

Comments: This species is closely allied to *S. reducta* and *S. acuta* as noted in the introduction. The similarities lie in the structure and chaetotaxy of segment 7, the structure of the male genitalia and the large size of the genital vesica and apodemes. In addition, the female genitalia of this species and *S. acuta* are similar except for the size of the cerci. This species in known only from California and Montana.

Specimens examined:

Holotype: ♂, Berkeley, California, April 17, 1948, W. W. Wirth. Allotype: ♀, same data. Types in the U. S. National Museum Collections. Paratypes: 7♂♂, 1♀, St. Marys, Montana, July 22–Aug. 2, 1935; 1♂ Logan Falls, Glacier National Park, July 18, 1935.

Swammerdamella reducta n. sp.

Males: Total length between 1.0 and 1.5 mm. (approximate, slide mounts). Color dark grey-brown; head and scutum darker; tarsi paler than body. Antennae 9-segmented; maxillary palpi 0.10 mm. long. Supra-alar setae 13 or 14, in a regular row; subspiraculars 2 or 3.

Wings 1.10–1.17 mm. long; section 3 of costal margin seven times as long as section 2; vein M 1.75–2.25 times as long as M_1.

Tergum 6 entirely unmodified (fig. 4I). Segment 7 (fig. 3C) much like that of *S. bispinosa* but lacking the additional median spine on the tergum and the complex emargination of the posterior margin of the sternum. Genital vesica and apodemes 0.27–0.31 mm. long. Genitalia (fig. 1I) much like those of *S. bispinosa* except for the more truncate posterior margin.

Females: Unknown.

Specimens examined:

Holotype: ♂, Alabama (no further data other than No. 2245), J. M. Aldrich. Type in the U. S. National Museum Collections. Paratype: ♂, LaFayette, Indiana, Sept. 9, 1916.

Swammerdamella mojingae n. sp.

Male: Total length 1.10 mm. Color black, feebly shining; all tarsi paler, yellowish grey; wings pale grey. Maxillary palpi 0.14 mm. long; antennae dull black with silvery pubescence, 10-segmented. Supra-alar setae 7, not in a definite row; 1 or 2 subspiraculars. Setae very sparse on anterior spiracular plate.

Wings 0.90 mm. long; section 3 of costal margin seven times as long as section 2; vein M twice as long as M_1.

Tergum 6 unmodified, neither produced nor inflexed; sternum 6 with a small, posteriorly rounded, posteromedial lobe. Tergum 7 without a median spine; sternum 7 with only a few lateral setae (fig. 5J). Genital vesica and apodemes 0.22 mm. long. Genitalia (fig. 5K) wider than long, without penis valves; aedeagal plate long and stout; gonocoxites somewhat mandibulate in appearance.

Females: Unknown.

Comments: This species shares with *S. magnifica*, *S. pygmaea* and *S. confusa* the presence of 10 antennal segments. Its tergum 7 lacks a median spine as does that of *S. pygmaea*. It is, however, as distinct from the North American and north European species as *S. magnifica*.

Specimen examined:

Holotype: ♂, Mojinga Swamp, Ft. Sherman, Canal Zone, June 17, 1952, F. S. Blanton. Type in the U. S. National Museum Collections.

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THE BLOWFLIES OF CALIFORNIA (Diptera: Calliphoridae) by MAURICE T. JAMES, Bulletin of the California Insect Survey, Vol. 4, no. 1, 34 pp. illus. University of California Press. $0.50.

This is another publication of a series designed to permit the identification and show the distribution of the insects of California. The three subfamilies, 16 genera, and 37 species of the family in California are keyed and synonymy, collection data, and notes on biology given. The collection data are very complete and in the case of the commoner species it is difficult to get a clear picture of the distribution without considerable effort, or a thorough familiarity with the geography of California. It would seem very desirable to include a series of maps that would present the distribution in graphic form, at least for the more abundant species. There are some corrections in type data and some new synonymy.

ALAN STONE.

THE GENUS SEIOPTERA KIRBY (DIPTERA, OTITIDAE)[1]

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The species of *Seioptera* were treated in 1941 by Hennig, who discussed the taxonomic position of the genus and described two new species in addition to the three species, *S. vibrans* (Linnaeus), *S. colon* Loew, and *S. dubiosa* Johnson, which he considered to be the only other known species.

Harriot in 1942, apparently unaware of Hennig's work, presented notes on the genus, including a key to four species, the three older species mentioned above and one which he described as new but which is obviously *S. albipes* Cresson.

We thus have six known species of *Seioptera*, four of which are found in North America. I have been able to examine specimens of all of the North American species. By correlating the results of my examination of this material with the data offered by Hennig, I am able to present the following key and notes in the hope that they will clear up some of the confusion that has existed and give a better picture of the group. One character, that of the nature of the vestiture of the mesopleura, has not been used previously, but it is one which I find of prime importance.

Two of the species, one of which, *S. vibrans* (L.), is a widespread species of holarctic distribution, and the other one of which, *S. colon* Loew, occurs in North America, differ in a number of ways from the others. These species constitute the typical subgroup.

Three species, *S. demonstrans* Hennig, from Manchuria, and the eastern North American forms, *S. albipes* Cresson and *S. dubiosa* Johnson, are rather closely related and form a second subgroup.

A third subgroup is formed by *S. importans* Hennig, from central Chile.

The above groupings together with some of the characters upon which they are based may be tabulated as follows:

	Bristles *mspl*[2]	*stpl*	*sa*	First Vein	Vestiture of Mesopleura
vibrans	0	2	0	0	pile
colon	0	2	0	0	0
demonstrans	0	2	0	hairy	setae
albipes	0	2	1	hairy	setae
dubiosa	0	2	1	hairy	setae
importans	1	1	2	0	setae

Hennig (1935) summarizes what is known of the biology of the genus as represented by the one relatively abundant species, *S. vibrans*, as follows: "Larvae normally (in Europe) saprophagous in rotting Narcissus bulbs, tomatoes, horse manure, and similar substances. They caused in England in the winter and early spring of 1925–26 considerable damage to the roots of vegetable and ornamental plants." Séguy (1950) states that the adults of *S. vibrans* devour aphids and leafhoppers ("pucerons et cicadelles") on the leaves of maple and linden trees. The immature stages have apparently never been described.

Genus **Seioptera** Kirby

Seioptera Kirby, 1817, *in* Kirby and Spence, Introd. Entom. 2: 305; Cresson, 1919, Proc. Acad. Nat. Sci. Philadelphia 71: 191; Curran, 1934, Fam. Gen. No. Amer. Diptera: 277; Hennig, 1939, *in* Lindner, Die Fliegen d. pal. Reg. 5 (fasc. 46/47): 69; Hennig, 1941, Arb. morph. tax. Entom. Berlin-Dahlem 8: 73; Harriot, 1942, Jour. New York Entom. Soc. 50: 195; Crampton, 1944, Proc. Entom. Soc. Washington 46: 153.

Seoptera Loew, 1867, Berlin. Entom. Zts. 11: 295; Loew, 1873, Smithsonian Misc. Collns. 256 (Monogr. No. Amer. Dipt. 3): 151; Aldrich, 1905, Smithsonian Misc. Collns. 46 (Cat. No. Amer. Dipt.): 597; Williston, 1908, Man. No. Amer. Dipt., ed. 3: 278; Hendel, 1910, Gen. Ins., fasc. 106: 69; Séguy, 1934, Faune de France 28: 82; Brues, Melander, and Carpenter, 1954, Bull. Mus. Comp. Zool. 108: 369.

Myodina Robineau-Desvoidy, 1830, Essai Myod.: 727; Schiner, 1864, Fauna Austriaca 2: 84; Röder, 1881, Berlin. Entom. Zts. 25: 209; Becker, 1905, Kat. pal. Dipt. 4: 105.

Generitype—*Tephritis vibrans* Latreille (= *Musca vibrans* L.), by monotypy. Hennig (1939) discusses the view of Coquillett that *Seioptera* is a synonym of *Ortalis*.

KEY TO THE KNOWN SPECIES OF *SEIOPTERA*

1 (4). Mesopleura either entirely bare or with fine white pile which is usually perceptible only from strongly oblique view; wings with first posterior cell strongly narrowed, at tip no more than slightly wider than length of *ta*; first vein without hairs; 2 *stpl*; O *sa*; fore basitarsi usually wholly blackish, but sometimes pale near base.

2 (3). Mesopleura with rather dense, extremely fine, white pile; wing with humeral cell hyaline, stigma blackish; part of apical wing spot posterad of third vein strongly tapering distally; facial carina straight in profile (Holarctic) ..... **vibrans**

3 (2). Mesopleura entirely bare; humeral cell and base of costal cell dark brown, stigma yellow; part of apical wing spot posterad of third vein more diffuse and less tapering distally; facial profile concave (Eastern North America) ..... **colon**

4 (1). Mesopleura with short but coarse blackish or dark brown hairs, in one species also with a

[1]Accepted for publication, Dec. 21, 1954.

[2]Explanation of abbreviations. Bristles: *acr*, acrostichal; *dc*, dorsocentral; *f*, frontal; *h*, humeral; *mspl*, mesopleural; *ntpl*, notopleural; *oc*, ocellar; *pa*, *prealar*; *po*, postocellar; *sa*, supraalar; *sc*, scutellar; *stpl*, sternopleural; *vte*, outer vertical; *vti*, inner vertical. Wing venation; *ta*, anterior cross-vein; *tp*, posterior cross-vein.

distinct bristle; first posterior cell apically parallel-sided or nearly so, at tip approximately twice as wide as length of *ta*.

5 (6). Mesopleura with a distinct bristle; first vein without hairs; 1 *stpl*; 2 *sa* (Chile) . . . **importans**

6 (5). Mesopleura without bristles; first vein with distinct hairs, at least apically; 2 *stpl*; 1 or O *sa*; anal cell without minute apical point; fore basitarsi yellowish to whitish.

7 (8). Without *sa*; wings 0.375 as broad as long (from base of humeral crossvein); apical spot extending 0.43 of distance from wing tip to *tp*; humeri and femora black (Manchuria) . . . . . **demonstrans**

8 (7). With 1 *sa*; wings 0.40 as broad as long (Eastern North America).

9 (10). Humeri and legs yellow; wings with brown streak in marginal cell just apicad of furcation of second and third veins; apical spot extending no more than 0.40 of distance from apex to *tp*; frontal orbits rather broadly pruinose anteriorly, narrowly shining posteriorly . . . . . **dubiosa**

10 (9). Humeri and femora black; marginal cell entirely hyaline; apical spot extending halfway to *tp*; frontal orbits without pruinosity, shining more than halfway to middle line of frons . . . . . **albipes**

Seioptera albipes Cresson

(Fig. 1)

Seioptera albipes Cresson, 1919, Proc. Acad. Nat. Sci. Philadelphia 71: 192; Leonard, 1928, Cornell Univ. Agric. Expt. Sta. Mem. 101: 851; Brimley, 1938, Ins. North Carolina: 382.

Seioptera currani Harriot, 1942, Jour. New York Entom. Soc. 50: 196.

This species has escaped the notice of both Harriot and Hennig. The characters cited in the key and shown in the figures should make *S. albipes* easily recognized. I have seen material, including the types of *albipes* and a paratype of *currani*, from the following localities: QUEBEC: (Abbotsford); NEW YORK (Ithaca); MICHIGAN (East Lansing); ILLINOIS (Alto Pass; Dubois); OHIO (Athens County); KANSAS (Douglas County); MISSISSIPPI (Oxford); GEORGIA (Atlanta). Brimley records it from Bryson City, North Carolina, and the type of *currani* is from Tuxedo, New York.

Seioptera colon Loew

Seoptera colon Loew, 1867, Berlin. Entom. Zts. 11: 296, pl. 2, f. 6; Loew, 1873, Smithsonian Misc. Collns. 256 (Monogr. Dipt. No. Amer. 3): 152, pl. 9, f. 6; Smith, 1910, Ann. Rept. New Jersey State Mus. for 1909: 800; Johnson, 1910, Psyche 17: 254.

Seioptera colon (Loew) Cresson, 1919, Proc. Acad. Nat. Sci. Philadelphia 71: 192; Curran, 1926, *in* Criddle, 56th Ann. Rept. Entom. Soc. Ontario: 103; Strickland, 1938, Canad. Jour. Res. (D) 16: 203 (erroneous record, corrected by Strickland, 1946, *ibid.* (D) 24: 165); Harriot, 1942, Jour. New York Entom. Soc. 50: 195.

It is hard to say how many of the above records are reliable, but it is certain that although *S. colon* was the first of its genus to be reported from North America it is still very scarce. Cresson considered the species a synonym of *S. vibrans*, but it is likely that he never saw *S. colon*. The Loew types were from "New York" and "Illinois." Harriot reported upon New York specimens which are part of the lot sent to Loew. The Smith, Johnson, and Curran citations refer respectively to records from New Jersey, Massachusetts, and Manitoba. I have seen a total of six specimens from the following localities: ILLINOIS (Bluffs, Aug. 19, 1917, in Ill. Nat. Hist. Surv.); VERMONT (White Mountains, July 11, in U. S. Nat. Mus.); DISTRICT OF COLUMBIA (Washington, Aug., in Univ. Kansas); MARYLAND (Glen Echo, June 25, 1922, J. R. Malloch, in U. S. Nat. Mus.); MISSISSIPPI (Oxford, May, 1945, F. M. Hull, in my collection).

Seioptera demonstrans Hennig

Seioptera demonstrans Hennig, 1941, Arb. morph. tax. Entom. Berlin-Dahlem 8: 75, ff. 3, 5.

Known only from the type localities: Sjaolin and Gaolinszy, Manchukuo (W. Alin), in the Deutsches Entomogisches Institut.

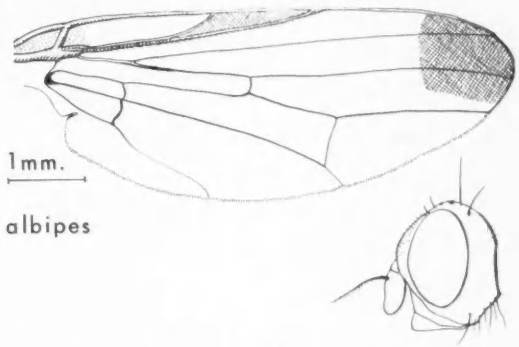


FIG. 1. *Seioptera albipes* Cresson, wing and head, male, Oxford, Mississippi.

Seioptera dubiosa Johnson

(Fig. 2)

Seioptera dubiosa Johnson, 1921, Occas. Pap. Boston Soc. Nat. Hist. 5: 15; Johnson, 1925, *ibid.*, 7: 260; Johnson, 1927, Biol. Surv. Mt. Desert Reg., pt. 1: 217; Harriot, 1942, Jour. New York Entom. Soc. 50: 196.

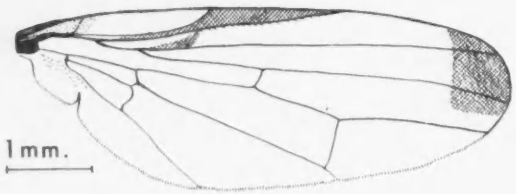
The Johnson references all cite a single female collected at Northeast Harbor, Mount Desert Island, Maine. Harriot gives notes on another female from Bar Harbor, also on Mount Desert. I have seen a single male from Red Deer River, Manitoba, August 3, 1937 (H. T. Peters), in the University of Kansas collection from which the following notes and the figure are drawn.

Head with lower occiput broad, rather swollen; front dull, except very narrowly on upper half of parafrontals; parafrontal whitish-pruinose stripes rather broad, especially anteriorly; front with moderate pale hair; parafacials wholly white-pruinose; arista with short but distinct pubescence; 1 *oc*, 1 divergent *po*, 1 *vti*, 1 *vte*, 1 very small *f*.

Thorax with dorsal pair of gray-pruinose lines very distinct; scutellum with yellowish rim; 2 small *stpl*; O *mspl*; 1 *h*; 2 *ntpl*; 1 *sa*; 2 *pa*; 1 *dc*; 1 *acr*; 2 *sc*; mesopleural hairs small and scattered, much as in *S. albipes*, but smaller and rather pale.

Wings as figured, humeral cell light yellow, stigma and apical spot brown, a brown streak in marginal cell from furcation of second and third veins to near tip of auxiliary vein; a few hairs on distal part of first vein as far back as apex of streak in marginal cell; anal cell with small but distinct point.

Abdomen yellowish basally.



dubiosa

FIG. 2. *Seioptera dubiosa* Johnson, wing, male, Red Deer River, Manitoba.

Seioptera importans Hennig

Seioptera importans Hennig, 1941, Arb. morph. tax. Entom. Berlin-Dahlem 8: 74, ff. 2, 4.

Known only from a single male from Central Chile (A. Faz), in the Deutsches Entomogisches Institut.

Seioptera vibrans (Linnaeus)

Musca vibrans Linnaeus, 1758, Syst. Nat., ed. 10: 599; Linnaeus, 1761, Fauna Suec., ed. 2: 459; Scopoli, 1763, Entom. Carniolica, No. 939; Schrank, 1781, Enum. Ins. Austr.: 470; Fabricius, 1781, Spec. Ins. 2: 450; Degeer, 1782, Mem. Ins. 6: 17, pl. 1, ff. 19, 20; Gmelin, 1788, Syst. Nat. 5: 2855; Fabricius, 1794, Ent. Syst. 4: 350; Geoffroy, Hist. Abreg. Ins. 2: 494; Schrank, 1803, Fauna Boica 3: 123.

Tephritis vibrans (L.) Fabricius, 1805, Syst. Antl.: 324; Latreille, 1809, Gen. Crust. Ins. 4: 355.

Seioptera[3] *vibrans* (L.) Kirby and Spence, 1817, Intr. Entom. 2: 305; Loew, 1867, Berlin. Entom. Zts. 11: 297 (*Seoptera*, emend.); Loew, 1873, Smithsonian Misc. Collns. 256 (Monogr. Dipt. No. Amer. 3): 153; Osten-Sacken, 1873, *ibid.*, corrections: I; Röder, 1881, Berlin. Entom. Zts. 25: 209; Brauer, 1883, Denkschr. Akad. Wiss. Wien Math.-nat. 47: 25; Karsch, 1887, Berlin. Entom. Zts. 31: 28; Mik, 1888, Wien. Entom. Ztg. 7: 94, 111; Aldrich, 1905, Smithsonian Misc. Collns. 46 (Cat. No. Amer. Dipt.): 598; Becker, 1905, Kat. pal. Dipt. 4: 105; Washburn, 1905, Univ. Minnesota Agric. Expt. Sta. Bull. 93: 117; Becker, 1907, Ann. Mus. Zool. Acad. St.-Petersburg 12: 271; Tucker, 1907, Kansas Univ. Sci. Bull. 4: 104 and Trans. Kansas Acad. Sci. 20: 200; Hendel, 1910, Gen. Ins., fasc. 106: 71, pl. 3, ff. 58, 60, pl. 4, f. 59; Smith, 1910, Ann. Rept. New Jersey State Mus. for 1909: 800; Van Duzee, 1911, Canad. Entom. 43: 244; Walker, E. M., 1913, Nat. Hist. Toronto Region: 396; Knab, 1916, Bull. Brooklyn Entom. Soc. 11: 46; Gibson, 1917, Ann. Rept. Entom. Soc. Ontario 47: 157; Cresson, 1919, Proc. Acad. Nat. Sci. Philadelphia 71: 192; Britton, 1920, Connecticut Geol. Nat. Hist. Surv. Bull. 31: 203; Gibson and Criddle, 1920, Ann. Rept. Entom. Soc. Ontario 50: 129; Cole and Lovett, 1921, Proc. California Acad. Sci. (4) 11: 330; Frey, 1921, Acta Soc. Flora Fauna Fenn. 48: 110; Johnson, 1925, Occas. Pap. Boston Nat. Hist. Soc. 7: 260 and Proc. Boston Soc. Nat. Hist. 38: 97; Sack, 1925, Abh. math.-nat. Abt. Bayer. Akad. Wiss. Suppl.: 275; Sturtevant, 1925, Jour. New York Entom. Soc. 33: 214; Cole, 1927, Proc. California Acad. Sci. (4) 16: 443; Johnson, 1927, Biol. Surv. Mt. Desert Reg., pt. 1: 217; Frost, 1928, Entom. News 39: 171; Leonard, 1928, Cornell Univ. Agric. Expt. Sta. Mem. 101: 851; Frost, 1929, Entom. News 40: 85; Johnson, 1930, Publ. Nantucket Maria Mitchell Assn. 3 (2): 150; Krogerus, 1932, Acta Zool. Fenn. 12: 115; Petch and Maltais, 1932, 24th Rept. Quebec Soc. Prot. Plants, suppl.: 56; Séguy, 1934, Faune de France 28: 82, ff. 117, 119, pl. 4, 42; Séguy, 1934, Mem. Acad. Cien. Exact. Zaragoza 3: 43; Kröber, 1935, Verh. Ver. Naturwiss. Heimatforsch. Hamburg 24: 46; Karl, 1936, Stettin. Entom. Ztg. 97: 109; Wnukowsky, 1936, Konowia 15: 121; Enderlein, 1937, Mitteil. Deutsch. Entom. Ges. 7: 73; Blanton, 1938, Jour. Econ. Entom. 31: 113; Brimley, 1938, Ins. No. Carolina: 382; Strickland, 1938, Canad. Jour. Res. (D) 16: 203; Hennig, 1939, *in* Lindner, Die Fliegen d. pal. Reg. 5 (fasc. 46/47): 70, pl. 6, f. 64, pl. 13, f. 164; Knowlton, Harmston, and Stains, 1939, Utah Agric. Expt. Sta. Mimeogr. Ser. 200 (Tech.), pt. 5: 10; Hennig, 1941, Arb. morph. tax. Entom. Berlin-Dahlem 8: 73; Harriot, 1942, Jour. New York Entom. Soc. 50: 195; Frey, 1949, Soc. Sci. Fenn. Comment. Biol. 8 (10): 28; Séguy, 1950, Encycl. Entom. (A) 26: 87, 89, 319, 508; Hennig, 1952, *in* Sorauer, Handb. Pflanzenkrankh., ed. 5, 5 (Lfg. 1): 103.

Ortalis vibrans (L.) Meigen, 1826, Syst. Beschr. 5: 284; Fallén, 1830, Dipt. Suec., Ortalides: 20; Macquart, 1935, Suites à Buffon (Hist. Nat. Dipt.) 2: 437; Zetterstedt, 1838, Ins. Lapp.: 747; Zetterstedt, 1846, Dipt. Scand. 5: 2159; Scholtz, 1849, Zts. Entom. Breslau, No. 9: 10; Walker, 1853, Ins. Brit., Dipt. 2: 197.

Myodina urticae Robineau-Desvoidy, 1830, Essai Myod.: 728.

Myodina vibrans (L.) Schiner, 1864, Fauna Austr. 2: 85; Rondani, 1874, Dipt. Ital. Prodr. 7 (Boll. Soc. Entom. Ital. 6): 5.

This species is by far the most abundant and widespread of the genus. Hennig (1939) lists the following palaearctic localities: Lapland, Finland, Sweden, Norway, England, Scotland, Ireland, Germany, France, Spain (Sobradiel, Zaragoza), Italy (Pavia, Milano, Val Susa, Bologna, Porto Civitanuova, Sondrio, Settino), Balkans (Siebenbürgen; Dalmatia), Forest of Bialowies, Kurland, Tomsk, Chinese Turkestan, Harbin, Ussuri Region. Frey (1949) records it from the island of Madeira. There is a specimen in the United States National Museum collected by Cockerell at Kongaus, Siberia.

In North America it was first recorded by Osten-Sacken (1873) on the basis of specimens from Massachusetts. Johnson (1925) notes specimens in the Harris collection taken at Cambridge, Mass., in 1935, and in Alabama. Aldrich (1905) mentions Idaho. I have seen material from British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Quebec, New Brunswick, Nova Scotia, Washington, Oregon, Idaho, Montana, Utah, Colorado, North Dakota, South Dakota, Minnesota, Wisconsin, Illinois, Indiana, Ohio, Michigan, New York, New England, and the District of Columbia. Besides these localities, Kansas, Pennsylvania, and New Jersey are listed in the literature.

[3]Since I have not been able to check all references, those with either the original spelling *Seioptera* or with Loew's emendation *Seoptera* are included here.

THE GENUS NEOEPHEMERA IN NORTH AMERICA (EPHEMEROPTERA: NEOEPHEMERIDAE)[1]

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With the discovery of a new species of *Neoephemera*, it seems advisable to review our present knowledge of all of the species of the genus and to construct keys for their separation. It is certainly likely that as our knowledge of the mayflies of North America is enlarged additional species of *Neoephemera* will be described; such a summary may, therefore, serve as a guide for future work.

McDunnough (1925) described *Neoephemera* from eight males that were collected by G. S. Walley at Laprairie, Quebec. In his paper, McDunnough gave no information relative to the phylogenetic relationship of the genus nor did he discuss conditions under which the specimens were taken. Ulmer (1933) was the first to give *Neoephemera* a family placement when he included it as one of the genera of the Ephemeridae. Subsequently, Needham, Traver, and Hsu (1935) erected a new subfamily, Neoephemerinae, to include McDunnough's genus as well as *Oreianthus*, a genus described by Traver in 1931. In this latter report, it was stated that the nymph of *Neoephemera* was unknown and that the distribution of the genus was Nearctic; *Oreianthus* was said to be Holarctic, and in the Nearctic to occur in the southeastern United States.

The description of *Oreianthus* was based on specimens collected and reared in 1929 and 1930. Traver (1931), in her description, indicated that the wing venation of the adult insect showed that it should be placed in the subfamily Ephemerinae even though the nymph, other than in size, resembles that of the genus *Caenis*. In discussing the relations of *Oreianthus* to other forms, Traver pointed out that, based on a study of illustrations, a nymph from the Garonne River in France, which was described by Joly (1870) as *Caenis maxima*, was in reality a member of her new genus. The status of Joly's nymph has still not been established with certainty by European workers nor, as far as I can determine, has the species again been recorded.

Because of similarities in appearance of the nymph of *Oreianthus* and that of *Caenis* and certain resemblances of the adults, Traver (1932) placed the former genus in the Baetinae, but indicated that the wing venation of the adult is similar to that of the Ephemerinae. In this same paper she mentioned that another species, represented only by nymphs, was at hand, and this same nymph was again reported by her in 1935 as occurring in Florida. In 1935, the genus was transferred to the family Ephemeridae, subfamily Neoephemerinae (Needham, Traver, and Hsu, 1935). The second species of *Oreianthus* was described from Florida nymphs by Traver (1937) but was not given a specific name, simply being designated as *Oreianthus* sp. No. 1.

Oreianthus was next discussed in "The Mayflies of Florida" (Berner, 1950) where it was said that phylogenetically the genus probably represented a distinct family.

Burks (1953) established the family Neoephemeridae to include the genera *Neoephemera* and *Neoephemeropsis* and at the same time synonymized *Oreianthus* with *Neoephemera*. When Ulmer (1939) described *Neoephemeropsis* from Sumatra and Java, he placed it in the family Potamanthidae and stated that it was close to *Neoephemera;* however, Burks claims that *Neoephemeropsis* almost certainly belongs in the family Neoephemeridae, a conclusion with which I am in agreement.

With the description of *Neoephemera youngi* Berner (1953), the status of Traver's *Oreianthus* sp. No. 1 was clarified. Subsequently, I have discovered a fourth species in the genus, the description of which is given below.

As presently understood, the genus in North America is distributed from southeastern Canada southward through the Appalachians to Florida and westward is known from Michigan. Nymphs and adults are rarely found in collections and records of the occurrence of the genus are sparse. The known distribution of each species will be discussed separately.

I am indebted to Dr. Henry Dietrich, Cornell University, and Dr. M. W. Sanderson, Illinois Natural History Survey, for the loan of specimens of *Neoephemera*. Mr. G. S. Walley, Division of Entomology, Ottawa, kindly provided me with a paratype of *N. bicolor*. All illustrations were prepared by Miss Esther Coogle, Staff Artist, Department of Biology, University of Florida.

Genus **Neoephemera** McDunnough

Genotype: *N. bicolor* McD., Laprairie, Quebec, July 9, 1924. No. 1292, Canadian National Collection.
Joly (1870, p. 142)—*Caenis*.
Eaton (1881, p. 196)—*Caenis*.
Eaton (1883, p. 140)—*Tricorythus* (?).
Lestage (1917, p. 373)—? *Tricorythus*.
McDunnough (1925, p. 168)—*Neoephemera*.

[1]This investigation was supported in part by a research grant, No. G-4058, from the National Institutes of Health, Public Health Service.
Date of acceptance, Oct. 4, 1954.

Traver (1931, p. 103; 1932, p. 111)—*Oreianthus*.
Ulmer (1933, p. 199)—*Neoephemera*.
Needham, Traver, and Hsu (1935, p. 289; p. 290)—*Neoephemera; Oreianthus*.
Traver (1937, p. 34)—*Oreianthus*.
Ulmer (1939, p. 484; p. 606)—*Neoephemera; Oreianthus*.
Berner (1950, p. 98)—*Oreianthus*.
Burks (1953, p. 42)—*Oreianthus* = *Neoephemera*.
Berner (1953, p. 145)—*Neoephemera*.

Wings hyaline; fore wings with basal costal crossveins weak or vestigal; stigmatic crossveins partly anastomosed; vein M_2 curved toward vein Cu_1 near the wing base; vein A_1 with from one to three crossveins attaching it to the hind margin (figs. 19, 20). Hind wing with an acute costal projection (fig. 18). Legs normal; claws dissimilar on legs. Pleural folds of abdominal segments expanded laterally. Penis short, dome-shaped; separated by a V-shaped median cleft on apical margin. Forceps with four segments, the two distal ones short (fig. 15). Three fully developed caudal filaments in both sexes.

Nymphs (fig. 9) grossly resemble *Caenis* but have two pairs of wing pads. Head almost twice as wide as long. Second segment of antennae covered with short, plumose hairs which are also present sparsely on vertex of head; such hairs are also present on the legs and abdomen. Prothorax longer at margins than at mid line, and margins may be considerably elongated at anterolateral angles (fig. 5); lateral margins developed into thin expanded areas. Body widest at greatest width of mesothorax. Submedian paired tubercules may be present at anterior margin of pronotum and mesonotum (fig. 4); short, posteriorly-projecting median tubercule on metanotum. Legs long and spider-like; claws simple, curved (fig. 11). Abdominal segment 1 with a pair of vestigal, filamentous gills; gills of segment 2 fused to form elytroid plates covering the following four pairs (fig. 9). Prominent median spine on tergites 1 and 2; tergites 2 to 8 may have a median carina which terminates in a short spine. Lateral margins of segments 3 to 9 prolonged posteriorly into flattened processes that may be decurved (fig.4); these processes exceptionally well developed on segments 6 to 9. Three caudal filaments with rings of stiff hairs at the joints.

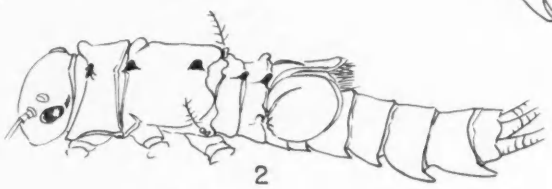
Neoephemera compressa n. sp.

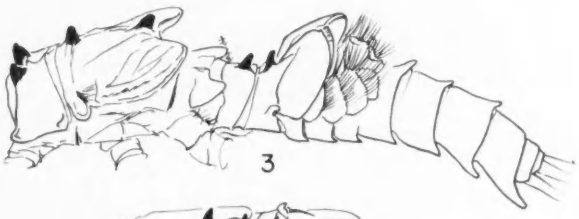
The adults of this new species can be separated from the others of the genus by size and venational characters or by color differences. *N. compressa* is distinct from the other two species in the size range in which it falls, *N. bicolor* and *N. youngi*, in the coloration of its legs and the absence of annulations on the caudal filaments. From *N. purpurea*, it may be separated by its smaller size and by the presence in the fore wing of only a single crossvein attaching A_1 to the hind margin. *N. compressa* also differs from *N. youngi* in lacking the small, dorsally-projecting, median spine on tergite 2.

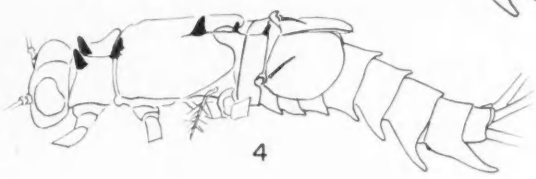
Male Holotype: Body length 9.8 mm.; mesothoracic wings 8.6 mm.; caudal filaments incomplete.

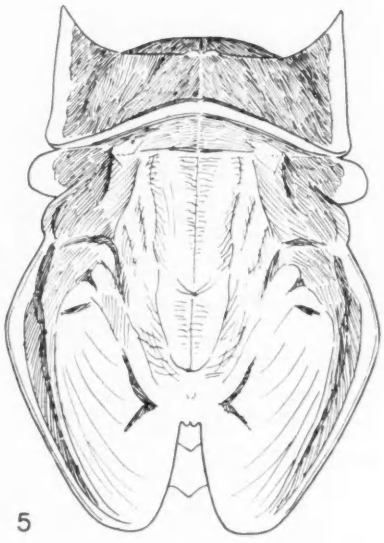
Head: Eyes large, separated by a distance equal to about one-half the width of one of the compound eyes. Vertex pale; geminate, deep-brown lines extending from posterior margin of lateral ocelli to occiput. Margin of occiput dark brown. Frontal carina brownish; dark brown marking at its distal end. Heavy brown horizontal marking below the antennae extending almost from the median carina laterally to the compound eyes. Antennae pale, marked with deep-brown, longitudinal line running length of second segment; flagellum with a slight brownish tinge. Ocelli brownish; basally with usual dark markings

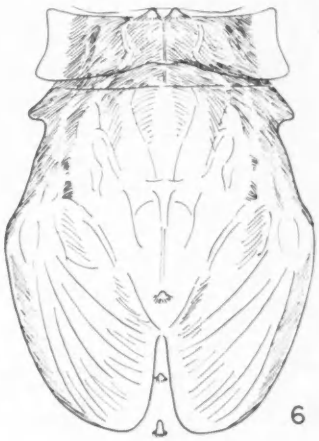
Thorax: Pronotum blackish brown around margins; very dark mid line; lateral portions slightly paler than the margins. Mesonotum much paler in color than the pronotum; blackish penciling around the margins of the scutum; scutellum pale in the median area and with blackish brown margins. Metanotum dark medially, paler laterally. Pleurae pale with dark, purplish-brown markings at the bases of the wings and legs. Sternum blackish brown but mottled with pale spots between the bases of each pair of legs; laterally brown. Prosternal tubercle blackish brown and projecting ventrally almost as far as the distal end of coxae. *Legs.* Fore coxa pale with blackish-brown spot on outer side; trochanter pale with purplish-brown penciling on outer surface; femur colored with intense purplish gray markings distally and pale in basal fifth; this basal pale area extending distally along the front margin about one-half its length; posterior margin colored deep purplish gray becoming much more extensive and covering remainder of femur. Tibia colored much the same as the femur, pale basally except for a short, longitudinal dark dash at the base; distal four-fifths purplish gray, except at the extreme end where it becomes pale once more. Tarsal segments 1 to 4 pale but washed with purplish gray, fourth dark at distal end, fifth segment much deeper in color with tendency to form a band in middle portion; claws shaded with purplish gray; first tarsal segment very short, about one-third the length of fifth, second and third equal, fourth slightly shorter than third, and fifth slightly shorter than fourth. Middle and hind legs colored very much as fore legs except for the fact that their coloration is even more intense. Pale area of femur less than that of fore femur; tibiae with a short dark dash at the base on the inner side. Tarsal segments with a tendency to form purplish rings on segments 2 to 5; fifth almost entirely purplish gray; claws as on fore legs. *Wings:* Hyaline and as

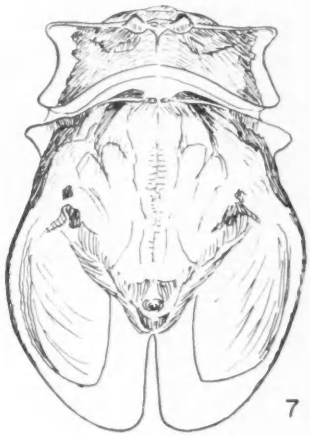


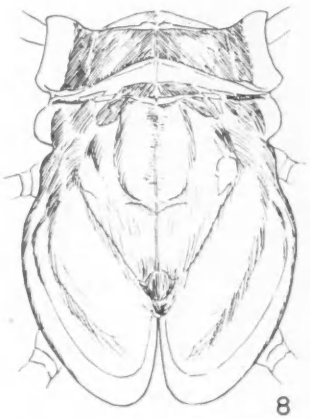












FIGS. 1–4. Oblique views of half-grown nymphs to show thoracic tubercules and abdominal spines.
1. *Neoephemera purpurea*. 2. *N. youngi*.
3. *N. bicolor*. 4. *N. compressa*.

FIGS. 5–8. Dorsal view of thorax of mature nymphs showing thoracic tubercules. 5. *N. purpurea*. 6. *N. compressa*. 7. *N. bicolor*. 8. *N. youngi*.

shown in figs. 22 and 23. All longitudinal veins pale; stigmatic area cloudy, crossveins anastomosed; single crossvein attaches A_1 to hind margin. Hind wing with a slight purplish-gray coloration at extreme base; costal projection so placed that it overlaps the anal crossvein probably providing a coupling device for the two wings when the insect is in flight.

Abdomen: Purplish brown dorsally; pale median line running the length of tergites 1 to 9; tenth completely dark. On tergite 2, the pale area expanding somewhat so that much of the median section is occupied by a pale area; on tergites 3 to 5 the median line expanding at the anterior margin into a broad pale area that runs along the anterior margin almost to the lateral line; on tergite 6 the expansion also occuring at the posterior margin and running laterally almost to the lateral border. Tergites 3 to 9 with small lateral, clear spots toward the posterior margin. Spiracular areas of segments 1 to 9 deeply colored with blackish brown. On the tergites in which the lateral margins are expanded, particularly 7 to 9, purplish brown coloration following the expansion; tenth tergite more or less uniformly colored with mottled purplish-brown; some intensification of color in the median line. Posterior margins of tergites 8 and 9 more deeply colored, pattern forming a blackish-brown band. Sternites much paler than tergites with a slight wash of purplish gray in the median area of 6 to 9 and laterally on 1 to 5. At the anteromedial line of the sternites, a deep blackish-brown mark which extends posteriorly as a streak on sternites 6 to 9; laterally on each of the sternites just below the dark marks of the spiracular areas, a deep, purplish-black mark that becomes progressively smaller posteriorly. Genitalia pale; as shown in fig. 16. Caudal filaments pale; basal segments with a slight brownish coloration.

FEMALE ALLOTYPE: Wing length 10 mm., body 9 mm. (abdomen of specimen in somewhat contracted state); caudal filaments 10 mm.

Head: Eyes widely separated. Vertex mottled; a deep, blackish-brown band on the occiput medial to the eyes runs across the head just above the median ocellus. Coloration of the head dark. Carina blackish brown in its distal portion. Coloration of head below antennae like that of male. Base of antenna pale, second segment marked as in male; flagellum brownish; tips broken in allotype.

Thorax: Marked much as in male except that mesonotum considerably darker with mid line blackish brown. Pleural and sternal markings similar to those of male. Prosternal process similar to that of male.

Legs: More intensely colored than in male with pale areas smaller than those of male. Tarsal segments appearing almost annulate in fore leg. Femora of middle and hind legs only slightly paler at the proximal end. Tibiae of middle and hind legs with small pale area basally, remainder deep purplish gray. Tarsal segments as in male, with color becoming more intense distally; first tarsal segment of middle and hind legs almost completely pale, washed with light purplish coloration.

Wings: Hyaline, some slight, purplish shading near the base; costal border with a faint purplish tinge; costa, subcosta and R_1 with purplish shadings, other longitudinal veins pale. Stigmatic veins weak and anastomosed.

Abdomen: Almost uniformly purplish brown with a faint indication of a pale median line beginning at the posterior portion of tergite 6 and running full length of 7 to 9; tergite 10 lacking this pale median line. Ventrally, sternites mottled with purplish coloration; a clear spot present at the anteromedian margin of segments 2 to 7. Lateral flanges deep purplish brown; caudal filaments washed with a purplish tinge.

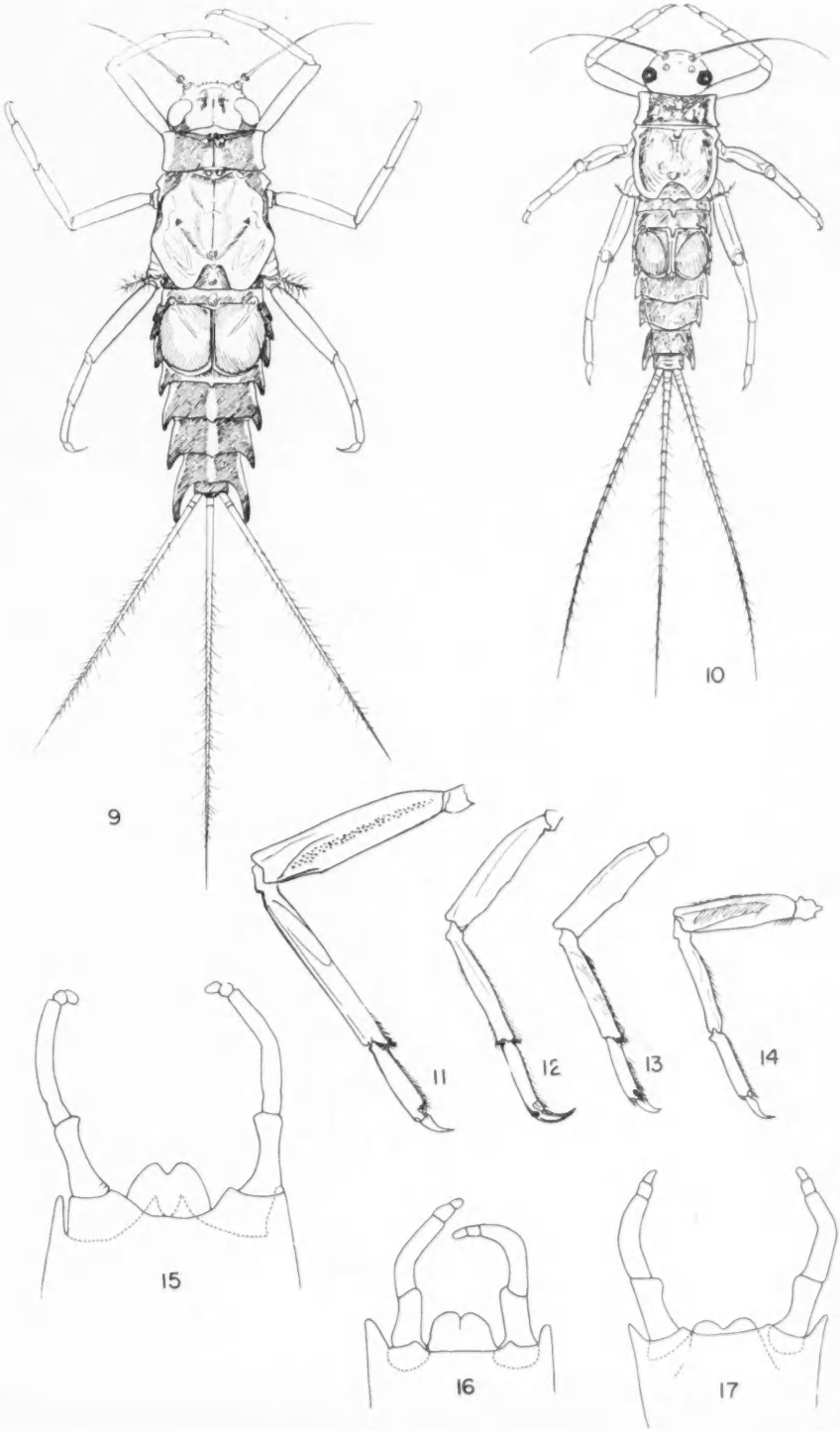
NYMPH: Body length 9 mm.; caudal filaments 8.5 mm.

Head: Vertex with numerous course hairs over the surface, some present on the medial surface of compound eyes. Hairs enlarged and frayed distally. Head crossed by purplish-brown band between the eyes; vertex brownish with two submedian clear spots; pale between ocelli. Ventrad to the antennae, between the eye and antennal base, a deep-brown band extending across the face. Basal segments of the antennae with the same type of course hairs that are present on the surface of the head; these hairs especially numerous on the second antennal segment where they give it a very rough appearance; flagellum pale and long.

Thorax: Lateral margin of pronotum as shown in fig. 6; most of the pronotum deep brown with flanges pale; pair of very prominent submedian tubercles at the anterior margin of pronotum. Mesonotum with anterolateral corners expanded into almost spine-like projections; a pair of minute submedian tubercules at anterior margin; a median spine present at the posterior margin between the wing pads. Mesonotum brownish, anterolateral corners dark brown. Metanotum completely concealed by wing pads. Sternum mottled with purplish-brown; a ventrally projecting process on the sternum between each pair of legs, prominent on the younger nymphs; on mature nymphs the projections clearly visible between the anterior and middle

EXPLANATION OF FIGURES

FIG. 9. *N. compressa*, half-grown nymph.
FIG. 10. *N. youngi*, half-grown nymph.
FIGS. 11–14. Right hind leg of mature nymphs. 11. *N. purpurea*. 12. *N. compressa*. 13. *N. youngi*. 14. *N. bicolor*.
FIGS. 15–17. Genitalia of male adults. 15. *N. purpurea*. 16. *N. compressa*. 17. *N. youngi*.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pairs of legs, but only a bump between the hind legs. A brown spot present on the sternum medial to each leg.

Legs: Covered with same type of hairs as seen on head and antennae. All segments of leg rather densely covered with these hairs, interspersed with long normal hairs on the femur and tibia. All legs long and spindly; purplish; femora more intensely colored at distal end; at the juncture of trochanter and femur, on the ventral side, a large brown spot overlapping both segments. Tarsus slightly paler at its proximal end; claw heavy and curved; pale except at tip where it becomes deep brown in color. Claws in striking contrast to the dark color of rest of the leg.

Abdomen: Abdominal segments expanded laterally into long, posterolateral projections, becoming more conspicuous on posterior segments where they are decurved. The posterior spine of each segment approximately half the length of that tergite, except that on 9 the spine equal to the length of the tergite. In older specimens the posterolateral spines clear at the outer margin and at the tip, but with purplish-brown coloration running into the posterior portion; anterolateral portion of the spines clear. The lateral margins of the segments covered with the same type of course frayed hairs present on the head. Tenth segment without postero-lateral spines. Tergites 1 and 2 with dorsally-projecting, pale median spines between the wing pads. The spine on segment 2 especially prominent and also covered with the course hairs. Tergites 6 to 8 free of gill covers, with posteriorly projecting spines at the median line; these spines much less conspicuous than those on tergites 1 and 2 and not erect. Abdomen deeply colored with purplish brown on the dorsum; ventrally paper with mottled appearance. The whole venter covered with coarse, frayed hairs. At the anterolateral margin of each of the sternites, a purplish-brown dash directed inward, the dash being less prominent but more elongate on the posterior segments and obsolescent on sternite 9. Caudal filaments approximately equal in length; brownish and with stiff, coarse hairs at the joints.

Younger nymphs are particularly striking in appearance and the name that I have given this species is derived from the pronounced dorso-ventral flattening of the thorax. The tubercules of the anteromedian margin of the pronotum are very conspicuous as is another pair at the anterior margin of the mesonotum. The single posterior tubercule of the mesonotum is also very prominent. As the nymphs mature, the thorax swells in size so that it assumes a more normal shape and the anterior tubercles are almost obliterated. The heads of younger nymphs are often completely pale except directly behind the eyes, where they are deeply colored with purplish brown. Legs of the young nymphs may also be paler basally instead of being wholly dark as in old nymphs. The posterolateral spines of the abdomen are one of the notable features of the young nymph. They also show a median line on the tergites which includes the posteromedial spines on segments 6 to 9. This light line is sometimes very pronounced. Because of the coloration of the posterolateral spines the abdomen may often appear to be banded at the margins.

Holotype: Male imago (reared), preserved in alcohol. Hamilton Co., Florida, Withlacoochee River at Georgia-Florida state line, March 14, 1954. Collected by L. Berner. In University of Florida collections.

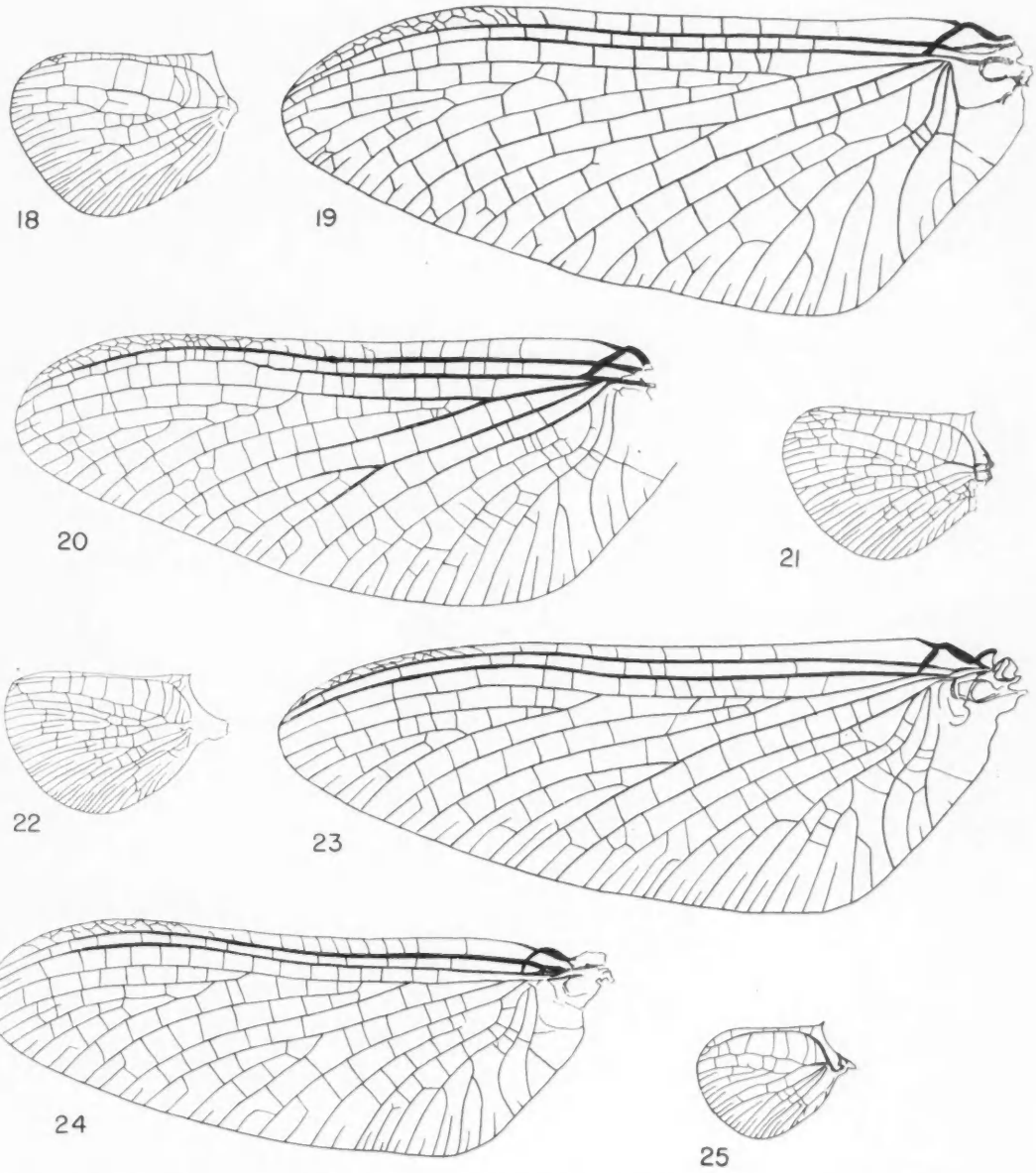
ALLOTYPE: Female imago (reared), preserved in alcohol. Same data as holotype. In University of Florida collections.

PARATYPES: 1 male subimago (partially shed); 4 females (reared). Same data as holotype. In University of Florida collections.

OTHER LOCALITY RECORDS: Florida, Withlacoochee River at several localities, January 28, 1954, (C. D. Hynes); Santa Fe River at Camp O'Leno State Park, October 31, 1953 (C. D. Hynes). Georgia, Ichawaynochaway Creek at Ga. Hwy. 91, November 27, 1953 (C. D. Hynes and L. Berner); Withlacoochee River, 4 miles west of Valdosta, March 13, 1954 (Hynes and Berner). All specimens in University of Florida collections.

The nymphs of *N. compressa* occur in streams of slow to moderate flow. The Withlacoochee River, where the nymphs were found in some abundance, is a deep, slow-flowing stream bordered by ash, willow, cypress and black-gum trees. Where the trunks of these trees are submerged, they are usually covered by a densely growing species of moss. It was in this moss that the nymphs were found, usually after a careful examination. They are slowly moving insects which are sometimes difficult to see in the dark vegetation and it is only by removing large clumps of the plant and shaking them that the nymphs are dislodged. Many were removed by picking them from the moss after it was taken from the water. The nymphs were associated with those of *Baetisca obesa*, which were very common in the moss. Amphipods and isopods were also numerous in this association. Nymphs were often found in some abundance by running a dip net through debris anchored in flowing water.

At the Ichawaynochaway Creek near Newton, Georgia, nymphs were taken by washing the submerged roots of plants which hang exposed at the banks. A few nymphs were also collected from logs which had been in the stream for a long period and had become very soft. The greatest number of nymphs from this stream were, however, taken from clumps of moss of the same species as that growing in the Withlacoochee



FIGS. 18–25. Wings of adults. 18–19. *N. purpurea*. 20–21. *N. bicolor*. 22–23. *N. compressa*. 24–25. *N. youngi*.

River. No nymphs were found in the swiftest part of the stream.

Adults were reared from mature nymphs collected from the Withlacoochee River in January and March. The earliest emergence occurred in late February and the latest was recorded in early April. The subimagal stage lasts approximately twenty-four hours.

My collections indicate that *N. compressa* may be a southern species restricted to streams of the Coastal Plain.

FIG. 26. The Withlacoochee River near Valdosta, Georgia, March 21, 1954. *Neoephemera compressa* nymphs were taken from the moss growing on the submerged trunks of these trees and from debris anchored in the stream.

Neoephemera purpurea (Traver)

Traver (1931, p. 103)—*Oreianthus purpureus*. Type in Cornell University Collections.
Needham, Traver, Hsu (1935, p. 291)—*Oreianthus purpureus*.
Traver (1937, p. 34)—*Oreianthus purpureus*.
Burks (1953, p. 43)—*Neoephemera purpurea*.

This species was described by Traver as *Oreianthus purpureus* in 1931. In her paper she gave a very complete description of both female imago and the nymph; however, in this earlier description one error was made which was later corrected in her 1937 report on the mayflies of the southeast. The description is entirely adequate and the 1937 correction simply makes note of the fact that she failed to mention the pair of low submedian tubercles on the anterior margin of the pronotum. Traver also pointed out that the short median tubercle on the mesonotum between the wing pads was, in the original description, in error described as being on the metanotum. The nymph is by far the largest of any of the North American species of *Neoephemera* and is readily distinguished from the others in the mature form by its size. The lateral profile of the nymph is distinctive as indicated in the drawing (fig. 1). The tubercules on the pro- and mesonotum are relatively short and inconspicuous on the mature nymph as compared with those of *bicolor* and *compressa*. On half-grown nymphs the tubercules are exaggerated but are still considerably less so than on nymphs of *N. compressa* at a comparable stage of development.

The specimens examined by Traver and reported on in publications subsequent to the original description have all represented mature nymphs. The appearance of a half-grown specimen is shown in fig. 1.

When Traver (1937) collected the nymphs of *N. purpurea* in North Carolina, she found them

usually beneath small, isolated boulders or irregularly-shaped sedimentary rocks in swift water, or under the large, flat rocks that form the main bed of the stream. Here she found only few specimens, never taking more than two or three nymphs from under a single rock. In 1948 while I was collecting in the North Fork of the French Broad River at Rosman, I found several half-grown nymphs of this species living in debris in slow-flowing water. A search of the larger rocks produced no specimens. During the summer of 1954, I again had an opportunity to collect mayflies in the mountain streams of North Carolina and at this time found nymphs of *N. purpurea* in Deep Creek and in the Nantahala River living commonly in debris caught in flowing water. Where bushes had fallen into the stream and had remained there for some time, the nymphs could be taken by dislodging the debris to which they were attached. In the Nantahala, as many as seventeen nymphs were taken at one time by gathering up clumps of exposed, clean-washed roots of vegetation in shallow water. The nymphs clung tenaciously but could be shaken or picked loose. A few nymphs were also collected by lifting large stones where the flow was swift and holding a screen downstream; however, this method of collecting was much more tedious and less productive than working in debris and roots.

Distributional records indicate that this species is confined to the swift streams of the Appalachian mountains.

Specimens examined: North Carolina, Davidson River, Pisgah Forest, (J. R. Traver), June 19, 22, 1929, C.U.[2]; June 30, 1930 (Holotype) C.U.; June 12–22, 1936, C.U.; North Fork of French Broad River at Rosman, August 19, 1948 (L. Berner) U.F.[2]; Deep Creek, Bryson City, August 12, 1954 (L. Berner) U.F.; Nantahala River, August 16, 1954 (L. Berner) U.F. Tennessee, Elkmont, October 10, 1940 (L. Giovannoli) U.F. Georgia, Neel Gap, June 8, 1945 (P. W. Fattig) I.N.H.S.[2]; Rock Creek, May 14, 1931 (P. W. Fattig), C. U.; Satolah, May 4, 1929 (J. G. Needham) C.U. Virginia, Piney River, August 1, 1953 (J. Pugh) U.F. West Virginia, Elk Garden, August 21, 1930, C. U.

Neoephemera bicolor McDunnough

McDunnough (1925, p. 168)—*Neoephemera bicolor*. Type in Canadian National Collections.
Needham, Traver, Hsu (1935, p. 289)—*N. bicolor*.

Through the courtesy of the Illinois Natural History Survey, I was privileged to study their collection of *Neoephemera*. Included in the lot of specimens was a small series of nymphs from Michigan identified by Dr. B. D. Burks as ?*Neoephemera bicolor* McD? These nymphs resembled those of *N. compressa* but differ in minor details as indicated in the key. Because of the presently known distribution of *N. bicolor*, I believe that Dr. Burks identification is correct and I am calling these specimens by that specific name.

The nymph of *N. bicolor* has never been described. I shall not detail the characteristics of the Michigan specimens as they are practically the same as those of *N. compressa* except in the following respects: the pronotal spines are more widely spaced and are slightly less prominent, and the posterolateral abdominal spines are slightly shorter and are less strongly curved ventrally. These details are shown in figs. 3, 4, 6, and 7.

Mr. G. S. Walley of the Division of Entomology, Ottawa, has kindly furnished me with a paratype and a topotype of *N. bicolor*. A comparison of these specimens with the three southern species has made it possible for me more clearly to delineate the forms in the key.

Specimens examined: Quebec, Laprairie, July 9, 1924 (G. S. Walley), paratype; July 7, 1925 (F. P. Ide). Michigan, Riffle River, Omer, May 21, 1936 (Frison and Ross)—nymphs.

There was no ecological information accompanying the nymphs of *N. bicolor* that were collected in Michigan. Because of their close resemblance to the nymphs of *N. youngi* and *compressa*, I believe that they occupy similar habitats, occurring in rivers and large streams that have a slow to moderate flow.

Neoephemera youngi Berner

Traver (1937, p. 83)—*Oreianthus* sp. No. 1.
Berner (1950, p. 99)—*Oreianthus* sp. No. 1.
Berner (1953, p. 145)—*Neoephemera youngi*. Type deposited in University of Florida Collections.

Among the specimens of *Neoephemera* in the collection of Illinois Natural History Survey, there is a single, adult male from Echeconnee Creek, Georgia, identified by Dr. B. D. Burks as *N. bicolor*. A careful examination of this specimen shows that it is in reality *N. youngi*. Apparently on the basis of this male, Dr. Burks (1953) reported that *N. bicolor* occurs in Georgia, a distribution which would have been unlikely as it is known elsewhere only from Michigan and Quebec. Further, Dr. Burks reported that *N. purpurea* occurs in Florida; intensive studies of the Ephemeroptera of this state have never produced a nymph of *purpurea* nor have I ever taken the species south of the Appalachians. It is my belief that *N. youngi* is essentially a costal plain species that may be much more widely distributed through this physiographic province than is indicated by specimens in collections.

N. youngi is closely related to *bicolor* and *compressa* and with these two species forms a clearly distinct unit of the genus *Neoephemera*. Size, venation, and characters of the immatures

[2]C. U.—Cornell University collections; U. F.—University of Florida collections; I.N.H.S.—Illinois Natural History Survey collections.

reveal this grouping very clearly as indicated in the keys to adults and nymphs.

Distribution and specimens examined: Generally distributed throughout northwest Florida from the Apalachicola River system westward. In Georgia from Decatur Co., Mosquito Creek, April 5, 1953, March 28, 1954 (L. Berner) U.F.; Town Creek, May 14, 1931 (P. W. Fattig) C.U.; Oconee River near Greensboro, April 9, 1931 (P. W. Fattig) C.U.; Upatoi Creek near Columbus, April 29, 1931 (P. W. Fattig) C.U.; Echeconnee Creek, 11 miles south of Macon, May 5, 1939 (P. W. Fattig) I.N.H.S. South Carolina, North Edisto River at Orangeburg, October 21, 1952 (H. P. Nicholson) U.F.

The habitats occupied by nymphs of *N. youngi* were discussed in some detail in "The Mayflies of Florida" (Berner, 1950) and will not be redescribed here. In many respects they are similar to those from which *N. compressa* was taken, although no *youngi* has ever been taken from moss around the trunks of submerged trees.

KEY TO NYMPHS

1. Body length (head to tails) 14–17 mm. Anterolateral projections of pronotum strongly produced (fig. 5); anterolateral projections of mesonotum prominent and rounded ..... **purpurea**
1'. Body length 8–10 mm.; anterolateral corners of pronotum only slightly elongated (fig. 6) 2
2. Posterolateral abdominal spines strongly produced (figs. 4, 9). Median spines present at posterior margins of abdominal segments 6–8 (fig. 4). Anterolateral corners of mesonotum pointed (fig. 6); pronotal submedian tubercules prominent (fig. 6) .. 3
2'. Posterolateral abdominal spines only moderately produced (fig. 2, 10). No median spines on posterior margins of abdominal segments 7 and 8 and only faintly indicated on 6 (fig. 10). Anterolateral corners of mesonotum rounded (fig. 8); pronotal submedian spines much reduced in mature nymphs (fig. 8) ..... **youngi**
3. Posterolateral abdominal spines strongly produced and curved ventrally (fig. 4). Pronotal submedian spines only slightly separated (fig. 6) ..... **compressa**
3'. Postero-lateral abdominal spines less strongly produced and less strongly curved ventrally (fig. 3). Pronotal submedian spines widely separated (fig. 7) ..... **bicolor**

KEY TO ADULTS

1. Wings 13.5 to 17 mm. in length; longitudinal veins of fore wings purplish black; two crossveins attaching A_1 to hind margin (figs. 18, 19) ..... **purpurea**
1'. Wings 8 to 10.5 mm. in length; veins, except those of costal border, pale. A single crossvein attaching A_1 to hind margin (fig. 20) 2
2. Small purplish band present in distal four-fifths of femora; tarsal segments 2 to 4 of middle and hind legs ringed with purplish-gray. Caudal filaments annulate ..... **youngi**
2'. Coloration of legs otherwise. Caudal filaments without annulations 3
3. Femora usually pale; tarsi smoky, not annulate. Each sternite with lateral black dot ..... **bicolor**
3'. Fore femur extensively colored with purplish-gray; tarsus purplish-gray, fifth segment with purplish-gray band. Other legs heavily shaded with deep purplish gray, tarsal segments annulate. Sternites with lateral black dot as well as a blackish-brown dot at anteromedial line ..... **compressa**

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Tenth International Congress of Entomology

Montreal, Canada,

August 17–25, 1956.

REVISION OF THE TWO-SPOTTED SPIDER MITE (Acarina, Tetranychidae) COMPLEX, TETRANYCHUS TELARIUS (LINNAEUS)[1]

H. BRUCE BOUDREAUX[2]

Nearly all previous taxonomic work on spider mites has been based upon morphologic characters. Even in the most recent and extensive revision of the group by Pritchard and Baker (1955), decisions concerning synonymy were largely made by observing resemblances in structure, since biological information was largely lacking.

The first attempt to establish the validity of two species by establishing the lack of interbreeding between them was made by McGregor and Newcomer (1928). This classic experiment is the basis for most of the attempts to decide upon the taxonomic status of tetranychid mites by employing biological data. The experiment is based upon the commonly known fact that virgin female spider mites produce only males, and mated *and fertilized* females produce both male and female offspring (with the exception of a few species which never produce males, *e.g.*, *Bryobia praetiosa* Koch and *Petrobia latens* Muller).

The cytological basis for this is known as haplodiploidy, in which the males develop from haploid (unfertilized) eggs with three chromosomes and females from fertilized eggs (diploid) with 6 chromosomes (Schrader, 1923). This type of reproduction (known as arrhenotoky) has been observed in seven species of tetranychid mites cultured in our laboratory, and is known in other mite families as well as in Hymenoptera, some coccids, a beetle, and in daphnids (White, 1954).

More recently, Keh (1952) indicated that *Tetranychus multisetis* McG. produced first generation hybrids with *T. bimaculatus* H. = (*telarius* [L.]) but succeeding generations are rarely produced. He concluded that *T. multisetis* was a subspecies of *bimaculatus*. In 1952, Davis was able to secure free interbreeding between *multisetis* and the carmine form of *bimaculatus* for several generations with no decline in fertility, but *T. hydrangeae* P. and B. failed to hybridize with either of the other species. Newcomer (1954) demonstrated by the same technique that *T. pacificus* McG. and *T. mcdanieli* McG. were distinct species in spite of the close morphologic resemblance between them. Iglinsky and Rainwater (1954) failed to produce females by crossing *T. desertorum* Bks. with *T. bimaculatus* H. = (*T. cinnabarinus* [Bois.]).

Because of extremely close resemblances among mounted specimens, both male and female, of common mites of the world, Pritchard and Baker (1955) list 43 synonyms of *T. telarius* (L.). Some of the names were based upon trifling variations, but *T. cinnabarinus* Boisduval, *multisetis* McG., *dianthica* Dosse and *cucurbitacearum* Sayed are based in part upon the fact that summer females are carmine in color, while *T. telarius* (L.) summer females are green. In spite of this color difference, no reliable morphologic differences have been demonstrated that distinguish the carmine forms from the green form except that *multisetis* is based upon the occurrence in females of two extra sensory setae on tarsus I and three extra sensory setae on tibia I of the females, and Dosse's (1952) illustration of *dianthica* and Sayed's (1946) of *cucurbitacearum* show the presence of setae as in *multisetis*. The males of all forms of the two-spotted mite complex are all similar in having these extra setae, but females of *telarius* and *cinnabarinus* normally lack these setae.

It is now evident that at least three species are involved in the two-spotted spider mite (*telarius*) complex, all of which may be distinguished from one another by constant morphologic characters of the female, although the males are extremely similar and more difficult to distinguish. The validity of these species is supported by experiments attempting to hybridize them with one another. One new name is proposed for a species which seems to be undescribed. The characters described are best seen through a phase-contrast microscope.

The descriptions which follow will serve to distinguish the species involved. All three species will key out to *T. telarius* in the key of Pritchard and Baker (1955). An extension of this key from the second member of couplet 23 on page 379, ending with word *telarius* follows:

FEMALES

1. Females with dorsal integumentary folds bearing semi-oblong lobes; basic color of live summer females green; eggs always white..... **telarius**

[1]This research was supported partly by the Freeport Sulphur Company and partly by the Louisiana Agricultural Experiment Station.

[2]Associate Professor of Zoology, Louisiana State University, Baton Rouge, Louisiana. The writer wishes to thank all who have contributed to the execution of this research. Especial thanks are due to L. D. Newsom who collected most of the mites I have examined, to A. E. Pritchard, who has re-examined his collection in the light of this revision and furnished distribution information, to E. W. Baker for his interest and encouragement and to J. H. Roberts and George H. Lowery for their critical review of the manuscript.

PAID PAPER. Accepted for publication, Nov. 8, 1955.

1. Females with dorsal integumentary folds bearing semicircular or triangular lobes; basic color of live summer females carmine; eggs often reddish..... 2
2. Ventral integumentary folds lacking lobes in the area bounded by the ventralmost hysterosomal setae; live summer females with four distinct dark spots; eggs always with some trace of red color .....**cinnabarinus**.
2. Ventral integumentary folds in the area bounded by the three pairs of pre-genital hysterosomal setae bearing lobes on the outer fold; live summer females with dark spots diffuse, not clearly marked; eggs from mated females white, from unmated females reddish.....**lobosus**

MALES

1. Anterior projection of knob of aedeagus rounded, posterior projection acutely pointed, upper surface of knob with slight indentation, axis of knob parallel with shaft.....**lobosus**
1. Anterior projection of knob of aedeagus acute or acutely rounded, upper surface of knob broadly rounded or broadly angulate, axis of knob forming a small angle with shaft or parallel..... 2
2. Anterior projection of knob of aedeagus very slightly rounded, axis of knob forming a small angle with the shaft, dorsum of knob broadly angulate .....**cinnabarinus**
2. Anterior projection of knob usually acute, upper surface usually rounded, angle of axis of knob with shaft very small or axis parallel.....**telarius**

Tetranychus telarius (Linnaeus)

Acarus telarius Linnaeus, 1758, Syst. Nat., I(10th edit.): 616. For full synonmy see Pritchard and Baker, 1955.

Eggs: Pale creamy or clear white when first laid, never reddish.

Adult summer female: Usually green in basic color, occasionally yellowish or dark green. Front of body anterior to eyes yellowish. Never carmine in basic color. A pair of dark trifid body markings, one mark at each side near the middle of the body, extremely rarely extending to the posterior end (fig. 1). Tarsus I with four tactile setae proximad to the proximal duplex setae, tibia I with nine tactile and one sensory setae (fig. 11). *Dorsal integumentary folds with semi-oblong lobes* at upper edge of folds (fig. 8). (*T. altanticus* McG. females have similar integumentary lobes, but have an additional pair of dark spots behind the lateral spots.) Ventrally the skin folds (striations) lack the lobes in the area bounded by the ventralmost setae (fig. 4).

Males: Aedeagus with a dorsally directed bend of about 90°, with the tip having small rather acute anterior and posterior projections, the upper surface broadly rounded or somewhat obtusely angulate, the axis of the enlargement about parallel with the axis of the shaft (fig. 5). Tarsus I with 4 tactile and two sensory setae proximad to the proximal duplex setae, and tibia I with nine tactile and four sensory setae. Integument without lobes on the folds. Males of this species are almost indistinguishable from those of *T. cinnabarinus*. The key characters are not always visible because the specimen must be examined from an exact lateral view.

TYPES: No type specimens of *T. telarius* are known, except those specimens described by other names but which have been declared synonyms in recent years, and which may be in various museums of the world. Specimens representing the present concept of the species have been deposited in the U. S. National Museum.

HOSTS: This species is highly omnivorous, and the host plant list is rather long. Dr. Pritchard has informed me (*in litt.*) that his specimens of this species represent collections from the United States, Europe, South Africa, Ceylon, South India, New Zealand and South Australia.

REMARKS: This species readily forms hybrids with *T. cinnabarinus*. In 22 laboratory crosses (12 using *telarius* ♀ x *cinnabarinus* ♂, and 10 reciprocal crosses, 636 males were produced, and there occurred 263 hybrid females. Three of the crosses involved the "multisetis" type of *cinnabarinus* and the other 19 employed the typical form. The hybrid females were a pale pinkish red, and they fed very little. Their life span was more than twice as long as the normal life span of either of the parent species. One hundred and sixty four of these hybrids were closely watched, and only four of them laid eggs, nine of which became males although the four females had mated with one or more of their "brothers."

Of the nine males so produced, one sired 23 female offspring, none of which laid eggs; one sired 4 females, one of which laid 8 sterile eggs; two males sired no female progeny and three were not tested. The hybrid females possessed lobes on the striae of the dorsum which were mostly triangular to semicircular, like those found in *cinnabarinus*, but there occurred occasional oblong lobes as in *telarius*. The male progeny of

EXPLANATION OF FIGURES

FIG. 1. *T. telarius*, typical appearance of dark food spots, dorsal view of female.

FIG. 2. *T. cinnabarinus*, typical appearance of dark food spots, dorsal view of female.

FIG. 3. *T. lobosus*, typical appearance of dark food spots, dorsal view of female.

FIG. 4. Ventral view of female mite. The area a-a bears lobes on the integumentary folds in *T. lobosus*, but not in *T. telarius* and *T. cinnabarinus*.

FIG. 5. Aedeagus of *T. telarius* male.

FIG. 6. Aedeagus of *T. cinnabarinus* male.

FIG. 7. Aedeagus of *T. lobosus* male.

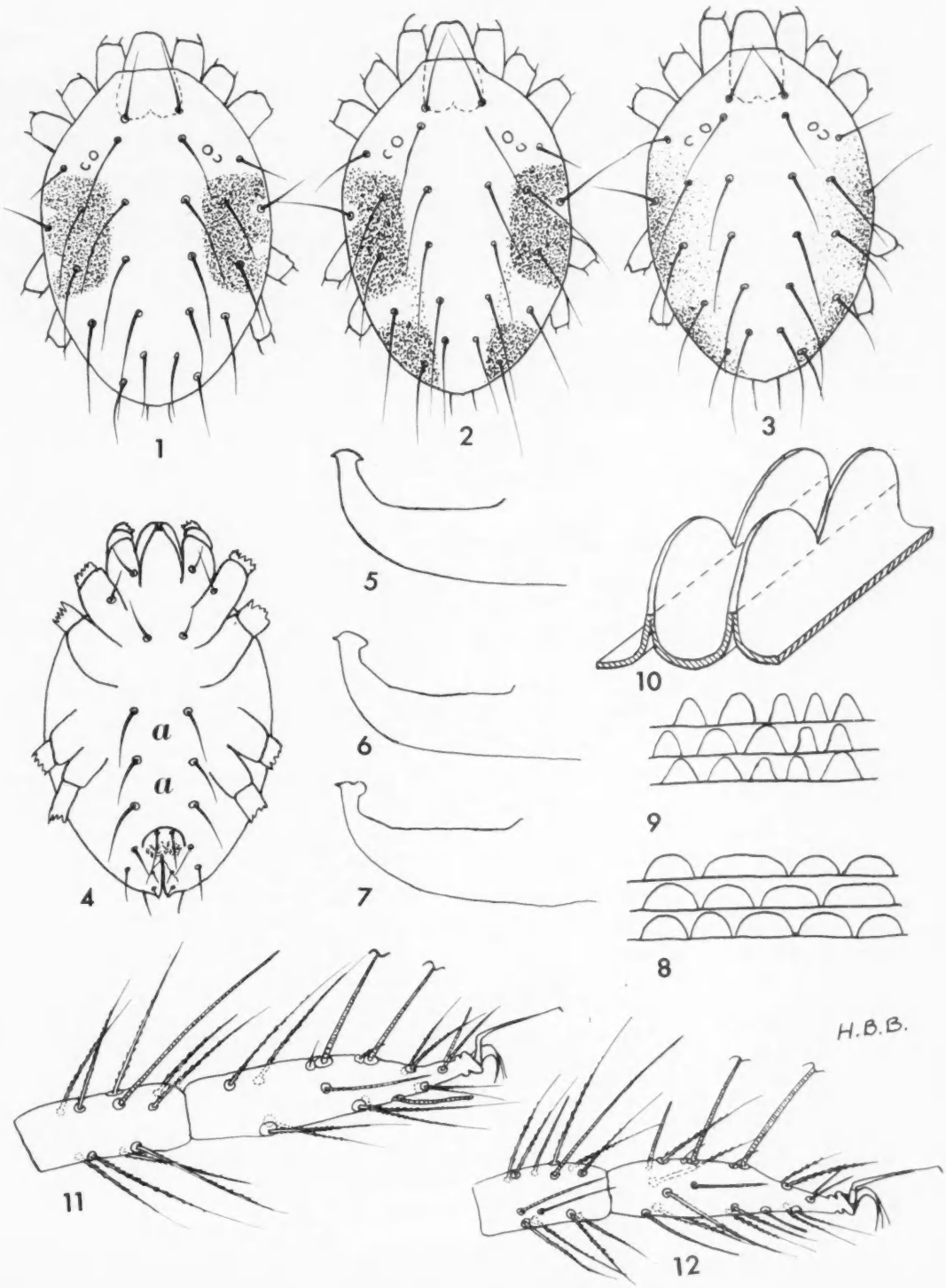
FIG. 8. Appearance of dorsal integumentary folds of *T. telarius* females, about 3000X.

FIG. 9. Appearance of dorsal integumentary folds of *T. lobosus* and *T. cinnabarinus*, about 3000X.

FIG. 10. Stereogram illustrating the nature of the integumentary lobes and folds in their natural position. Pressure of the cover glass on slide preparations bends the lobes so they appear as in Figs. 8 and 9. About 9000X.

FIG. 11. Setation of tibia I and tarsus I of females, typical of all three species except for variations in seta position.

FIG. 12. Typical polychaete condition of fore tibia and tarsus of some females of *cinnabarinus* ("multisetis") and of *telarius*.


1
2
3
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5
6
7
8
9
10
11
12
a
a
H.B.B.

these hybrids possessed no feature clearly inherited from either grandparent (see pedigrees, fig. 13).

Tetranychus telarius may only rarely hybridize with *T. lobosus*. In eight such crosses, 321 males and 1 female were produced. This female died before she could be tested for fertility. She was similar to the *telarius-cinnabarinus* hybrids, and possessed lobes on the ventral striations, as does *T. lobosus*.

Recently specimens from Arkansas were collected on cotton which bore extra setae on the fore tarsi and tibiae as in the "multisetis" type of *cinnabarinus*. Otherwise they were indistinguishable from *telarius*. This polychaete form is being cultured for genetic studies. One specimen among several received from a culture in Maryland (Floyd F. Smith) was a female with a single extra sensory seta on one tarsus. The other females received were normal.

Tetranychus cinnabarinus (Boisduval)

Acarus cinnabarinus Boisduval, 1867, Essai sur l'Ent. Hort, p. 88. Paris.
Tetranychus multisetis McGregor, 1950, Amer. Midl. Nat., 44(2): 294. *New synonymy.*
Tetranychus urticae dianthica Dosse, 1952, Hofchen-Briefe, 5: 250. *New synonymy.*

Boisduval's name appears to be the first which applies to this carmine species of mite. That the European carmine mites are of this species is evident from the fact that females of *dianthica* Dosse have the same foreleg chaetotaxy as *multisetis* McG., and *multisetis* freely interbreeds with *cinnabarinus* (Davis, 1950, and confirmed by the writer) in this country. This supposition is also the opinion of Dr. A. E. Pritchard (*in litt.*), who has confirmed it in examining his specimens from Europe and other sources. T. *cucurbitacearum* Sayed may be synonym of this species, but specimens were not examined by the writer.

Eggs: Always with a trace of red. The color is more intense in eggs from unmated females.

Adult summer female: Basic color carmine red, the carmine color restricted to the body behind the eyes, with the anterior part yellowish. Four dark body spots laterally, the anterior pair larger, the posterior pair near the anal area (fig. 2). Tarsus I with four tactile setae proximad to proximal duplex setae, tibia I with nine tactile and one sensory setae. Rarely some populations bear setae as in the males (*dianthica* Dosse and *multisetis* McG., fig. 12). *Dorsal integumentary folds with semi-circular or triangularly rounded lobes on edge of outer folds* (fig. 9). Ventrally the skin folds lack these lobes, as in *telarius* (fig. 4).

Males: Aedeagus as in *telarius*, except that axis of the knob always forms a slight angle with the shaft, the anterior angulation is slightly rounded and the upper surface of the knob is obtusely angulate (fig. 6). Tarsus I with four tactile and two sensory setae proximad to the proximal duplex setae, and tibia I with nine tactile and four sensory setae.

TYPES: No type specimens of this species are known except those of "multisetis" McGregor in the U. S. National Museum. Specimens representing the present concept of *T. cinnabarinus* have been deposited in the U. S. National Museum.

HOSTS: Known host plants of this species are very numerous, and it seems also to be omnivorous. It is an important pest of many plants.

DISTRIBUTION: Dr. Pritchard informs me (*in litt.*) that his specimens of this species are from the United States, Europe, Israel, Turkey, Argentina and Japan. This is the carmine species which is often found in greenhouses in more northern temperate regions.

REMARKS: This species forms mostly sterile hybrids with *telarius*, but eight attempts at crossing it with *lobosus* produced 257 males and no female offspring.

Tetranychus lobosus new species

Eggs: When laid by mated females, the eggs are clear or creamy white. These white eggs hatch either into males or females. Eggs from virgin females are reddish, but virgin females which have laid reddish eggs will lay white eggs after mating, and these white eggs produce both females and males, while the reddish eggs laid before mating all hatch into males.

Adult summer female: Color in life deep carmine red, with dark food spots diffuse and indistinct, but forming two long darker areas on sides of body, extending to the posterior end (fig. 3). Carmine color covering entire body except stylophore and legs. Tarsus I with four tactile setae proximad to the proximal duplex setae, but three of these are nearer the duplexes than the other; tibia I with nine tactile and one sensory setae. *Lobes on edges of dorsal skin folds semicircular to triangularly rounded; ventrally, oblong lobes are present in the area bounded by the three pairs of ventralmost hysterosomal setae*, thus differing from *telarius* and *cinnabarinus* females (fig. 4).

Males: Aedeagus as in the other species, except that the anterior projection of the knob is rounded, the knob bears a depression dorsally, and its axis is parallel with that of the shaft (fig. 7). Setation of forelegs as in the other two species. The empodial spurs of legs III and IV are more slender than the stouter spurs of the other two species.

HOLOTYPE: Male, collected on cotton (L. D. Newsom) on July 18, 1955, at Grand Coteau, Louisiana.

ALLOTYPE: Female, collected on cotton (L. D. Newsom) on July 18, 1955 at Grand Coteau, Louisiana. Both types are in the U. S. National Museum.

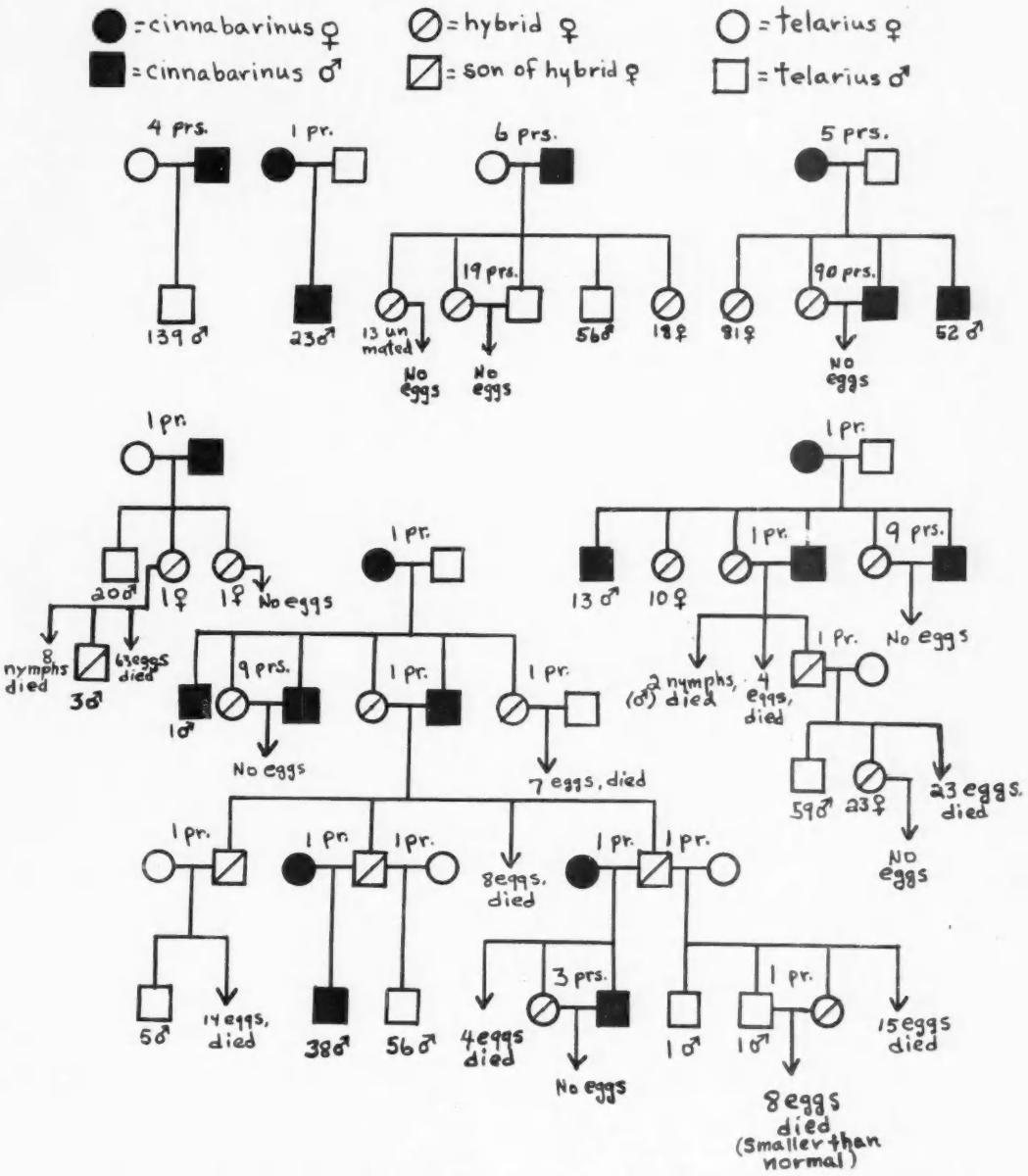

FIG. 13. Summary of hybridization attempts between *T. telarius* and typical *T. cinnabarinus*. It must be remembered that males have no fathers since they are produced parthenogenetically, and therefore they are of the same species as their mothers.

PARATYPES: In the collection of the writer.

HOSTS: This species seems to be omnivorous, as are the other two species. In Louisiana it has been collected on *Amaranthus*, *Ambrosia*, Bean, Blackberry, *Chenopodium*, Clover, Corn, Cotton, *Desmodium*, Eggplant, *Geranium*, *Gladiolus*, *Hibiscus*, Morning glory, Passion flower, Soybean, Strawberry, Violet and *Xanthium*. Dr. Pritchard has specimens from *Wisteria* collected in Durham, North Carolina.

DISTRIBUTION: This mite seems to be restricted to the Southeast United States, possibly from Texas to Virginia.

DISCUSSION

The reciprocal crossing attempts mentioned above will be discussed fully with other hybridization attempts involving other species in another paper yet to be published.

Nonfeeding winter-type females of *telarius*, *cinnabarinus* and "multisetis" have been produced artificially by exposure of protonymphs and earlier stages to daily photoperiods of 8 hours at 56°–58° F. on cotton plants. The last two forms readily transformed into winter females, but *telarius* produced only a small number of winter females under these conditions. In the case of *telarius*, some of the females which became nonfeeding did not turn the bright orange characteristic color of this stage. These green females however, bore the "unbroken striae" characteristic of nonfeeding, nonlaying winter females as did also females of both types of *cinnabarinus* which also became bright orange. (See Pritchard and Baker, 1952.)

With this revision, it becomes evident that a vast amount of literature pertaining to the two-spotted spider mite (*T. bimaculatus* H.) in this country and *T. altheae*, V. H., *T. urticae* Koch, *inter alia*, in Europe and other parts of the world will need to be re-evaluated concerning the species involved. *T. telarius* occurs worldwide in colder temperate latitudes. *T. cinnabarinus* occurs over much of the warmer temperate zone and subtropics, and occasionally in northern greenhouses. *T. lobosus* seems to be restricted to the Southeastern United States. All three species are omnivorous and are of great economic importance. It is possible that there are still other species which are distinct, but which are still being confused with the common two-spotted mite complex.

As White (1954) has stated, in arrhenotokous species such as these are, nondetrimental mutations can quickly become established in a population since males can be considered to be "homozygous" for all practical purposes because of their haploid germ plasm. The morphologic agreement between the American *telarius* and the other *telarius* of the world (green mites) may only indicate very close relationship of sibling species. At any rate, published accounts of the biology of various populations, such as that of Linke (1953) who studied *telarius* (= *althaeae*) in Germany, are at variance with some of the observations that have been made in our laboratory. If mating experiments between the American and European forms indicate reproductive isolation, then the name *telarius* should be restricted to the European species, and the reproductively isolated forms will need revaluation as to specific status, since Linnaeus described *telarius* from Europe. The same might be true of *cinnabarinus*, since the name was used first for a population in France. In that case, *multisetis* McG. seems to be the first name applied to the carmine mites here described as *cinnabarinus*, and *bimaculatus* Harvey would perhaps apply to the American "telarius." It is possible that the assertion made by McGregor (1950), that the American "bimaculatus" is distinct from the European "althaeae", is based upon his misidentification of *cinnabarinus* and *lobosus* as *bimaculatus*.

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DESCRIPTION AND REARING OF VARIOUS STAGES OF DENDROPHAONIA SCABRA (GIGLIO-TOS)[1] (DIPTERA, MUSCIDAE)

ERNEST L. CALHOUN, H. R. DODGE, AND R. W. FAY

Dendrophaonia scabra (Giglio-Tos) is a native muscid fly which is known to have a wide distribution in the eastern United States. At times males may be found sunning themselves on tree trunks at the edges of woods, and the species has been considered to be a forest dweller.

Although heretofore considered scarce, this species recently has been demonstrated to breed commonly in privies in Georgia. (Kilpatrick and Schoof, in M. S.) Trap records from 100 selected urban, suburban and rural privies in the Savannah, Georgia, area for a 1-year period revealed that approximately 10 percent of the total flies trapped were *D. scabra* (= *D. hilariformis* (Stein)). The species was recorded in every month of the year with peaks of abundance in early spring and late fall. In 1948 one of the authors (H. R. Dodge) found adults frequenting a chicken coop at Montgomery, Alabama, and in 1953 in a guinea pig hutch in DeKalb County, Georgia. Adults also have been reared from sludge in garbage cans in Savannah, Georgia (Quarterman and Mathis, 1952). It is possible that this is a sylvan species which is becoming adapted to dwelling with man. In view of its possible medical importance as a breeder in human feces, an attempt was made to colonize the species in the laboratory.

GENERAL PROCEDURE

All work described was done under insectary conditions of 80° F. and 70 percent relative humidity. A stock colony was maintained in a 14 x 16 x 18 inch screened cage by adding pupae or adults as available. A mixture of powdered whole milk (12 oz.), water (3,680 ml.), and extracted honey (15 ml.) was available to the adult flies at all times. Eggs were deposited in sterilized cow manure which had been placed in pans in the colony cage. The eggs were transferred from the manure to a rearing medium consisting of NAIDM mash[2] (11 oz.), water (500 ml.), yeast suspension (226.8 gms. yeast in 750 ml. water) (45 ml.) and non-diastatic malt syrup (5 ml.), mixed and placed in a 1-gallon jar 24 hours previously. Pupae were picked by hand and placed in cages for emergence.

[1]From the Communicable Disease Center, Public Health Service, U. S. Department of Health, Education, and Welfare, Savannah, Georgia

[2]Bran and alfalfa meal (70 percent: 30 percent). Standard fly larval media manufactured by Ralston Purina Company, Checkerboard Square, St. Louis, Mo.

MATING AND OVIPOSITION

Adults in colony cages exhibited a swift, irregular, zigzag darting flight in contrast to the slower, more deliberate flight of house flies. Copulation was observed both in flight and while the female was resting on the cage walls. Pairs joining in flight rapidly fell to the cage floor. In all cases, the position of the male was above and facing in the same direction as the female. Copulation lasted only a few seconds.

Different media, tested individually and in combinations, showed that females were attracted to moist cow manure, fermenting NAIDM larvae-rearing medium, moist and broken rabbit feces, decomposing ground beef, empty fly puparia, sour milk on cellulose pads, and filter-paper disks moistened with a water extract of cow manure. Cow manure was the preferred oviposition medium when placed in competition with the other media mentioned above. Eggs were not deposited upon fresh ground beef but oviposition did occur when the beef showed considerable decomposition. Oviposition did not occur upon fresh milk pads, moistened unbroken rabbit feces, rotten wood, or fresh garbage composed of beef soup, bread and potato peels. Apparently *D. scabra* females are quite selective since egg deposition did not occur generally unless the media possessed a high moisture content, products of fermentation, and cracks or crevices as hiding places for the eggs. Seldom were the eggs laid fully exposed upon a flat surface.

In nine replications one female and two or three male flies, all of known age, were confined in a small holding cage and provided with fresh milk on a cellulose pad. A pan of moistened cow manure (1 square inch) was placed into each cage and minutely examined for eggs at 24-hour intervals. The eggs were generally found grouped in cracks of the manure. The largest number of eggs deposited per female in any one period was 170. In this instance the eggs were found in 12 different locations on the manure. Only 2 of the 170 eggs were found fully exposed; and the remainder were either completely hidden or protruding slightly from cracks in the medium. One group of 65 eggs was the largest number observed at a single oviposition site. It was not determined whether all the eggs found in one group were deposited at one time or by several visits to the particular site over a period of time. It was evident that eggs of this species are generally laid in groups, in

sites affording maximum protection,. and preferably in moist substrates supplying the necessary food requirements for larval growth and development.

The original wild flies trapped in privies shortly after emergence laid the first eggs 15 days after capture. Estimates of the preoviposition period for groups of flies from different batches of pupae (Table I) varied from 8 to 15 days with an average of 12.3 days.

In studies with nine individual females (Table II) the preoviposition periods varied from 6 to 25 days with an average of approximately 14 days. Based on the time of emergence, there is some indication of a biweekly periodicity in egg-laying peaks over an 8-week period with an average of 230 eggs per female.

TABLE I

LIFE CYCLE DATA FOR *Dendrophaonia scabra* REARED ON NAIDM MEDIUM UNDER INSECTARY CONDITIONS OF 80. F. AND 70 PERCENT RELATIVE HUMIDITY

DAYS TO FIRST PUPAE	PUPAL STAGE DATA				PRE-OVIPOSITION Period (days)	MINIMUM LIFE CYCLE (days)
	Pupae per Jar	Av. Weight per Pupa (mgs.)	Days to First Emergence	Percent Emergence		
13	26	15.7	4	57.7	8	25
11	78	19.8	5	64.1	10	26
10	76	17.4	6	60.5	15	31
9	154	16.8	8	20.8	14	31
9	57	—	8	52.6	12	29
10	66	16.3	7	31.8	15	32
9	128	16.7	8	89.1	*	*
10	184	12.7	7	29.9	*	*
10	75	18.8	6	93.3	*	*
Average 10.1	—	17.1	6.6	55.5	12.3	29

*Adults released into stock colony cage.

THE EGG STAGE

Description: The egg is cylindrical, 0.28 mm. in diameter, elongate, 1.18–1.24 mm. long, opaque white, and evenly tapered at both ends (figs. 11–13). The surface has a reticulated pattern and dorsally exhibits a pair of longitudinal ribs which are strongly explanate and continuous at the micropyle end. In lateral view the ventral margin is convex and the dorsal margin straight or slightly concave. Based on three replicate weighings of 100 eggs, the average weight per egg is 0.0257 milligrams.

Hatching: Eggs for hatching studies were collected on moistened manure and removed individually with a dissecting needle, counted, and placed upon a moist gauze pad in contact with moist larval-rearing medium. Counts, made at 24-hour intervals over a 5-day period, showed the greatest percentage of eggs to hatch on the second day after oviposition. The average total hatch was 64 percent (Table III).

THE LARVAL STAGE

Description: The larva is a typical muscoid maggot with a smooth, creamy white body of 12 apparent segments, tapering from the truncate posterior end to the minute cephalic segment. There are two prominent posterior spiracles on the last segment and an inconspicuous anterior pair, situated at the hind margin of the second apparent segment, each with 5 to 7 lobes. Anteroventrally the last seven segments bear spiculose locomotor pads, each of about five rows of spicules. There are three instars, each of which differs markedly in details of the cephalopharyngeal skeleton and the spiracles.

First instar. This instar is distinguished by the minute body (1.2 to 2.6 mm. in length), the black spicules of the locomotor pads, and by the absence of the anterior spiracles. The cephalopharyngeal skeleton (figure 1) is 0.42 mm. long and 0.088 mm. high, and has no definite hypostomal or dental sclerites. Instead there are two elongate rods connecting the pharyngeal sclerite to the mouthhooks. From the sides of these rods arise two poorly pigmented plate-like lobes.

Above these rods and parallel to them is an unpaired median rod extending forward from the pharyngeal sclerite. The apex of the mouth hook is articulated to it, and preceded by a series of 7 or 8 teeth, of which only two are shown in fig. 1. The posterior spiracles (fig. 4, 10) are each a rounded, sclerotized disc at the apex of a fleshy tubercle; the prominent tracheal trunk becomes rather forked at its extremity, thus there are evidently two spiracular slits. Surrounding the aperture of the spiracles is a fringe of dendritic hairs (fig. 10) which serve to hold the spiracular openings in the surface film if the larva is submerged. The body integument above the spiracles is distinctly mammillate (fig. 10) in this instar only.

Second instar. The body of the larva is still small (2.0 to 6.3 mm. in length) but this instar is readily recognized by the colorless spicules of the locomotor pads, the larger cephalopharyngeal skeleton (0.74 mm. long, 0.21 mm. high), the two definite transverse oval slits of the posterior

TABLE II

PREOVIPOSITION PERIOD AND RATE OF EGG DEPOSITION OF NINE FEMALE *Dendrophaonia scabra* UNDER INSECTARY CONDITIONS OF 80. F. AND 70 PERCENT RELATIVE HUMIDITY

FEMALE	PREOVIPOSITION PERIOD (days)	EGGS PER WEEK AFTER ADULT EMERGENCE									TOTAL EGGS
		1	2	3	4	5	6	7	8	9	
A	6	31	0	21	191	21	92	20	101	—*	477
B	8	0	156	98	88	—	—	—	—	—	342
C	9	0	167	0	1	0	158	—	—	—	326
D	11	0	58	37	72	24	—	—	—	—	191
E	12	0	117	91	18	128	45	52	7	50	508
F	14	0	121	0	70	—	—	—	—	—	191
G	16	0	0	4	0	—	—	—	—	—	4
H	23	0	0	0	3	14	—	—	—	—	17
I	25	0	0	0	9	13	—	—	—	—	22
Total per week		31	619	251	452	200	295	72	108	50	2078

*—indicates death of fly.

TABLE III

HATCHING FIGURES FOR *Dendrophaonia scabra* EGGS UNDER INSECTARY CONDITIONS OF 80° F.—70 PERCENT RELATIVE HUMIDITY

NUMBER EGGS IN BATCH	NUMBER OF EGGS HATCHING AT 24-HR. INTERVALS					TOTAL HATCH	PERCENT HATCH
	24	48	72	96	120		
12	—	6	—	—	—	6	50
60	1	21	10	—	—	32	54
80	21	20	5	—	—	46	57
36	—	24	—	—	—	24	67
80	32	24	3	—	—	59	74
120	29	44	6	2	3	84	71
60	13	16	4	1	—	34	58
448	96	155	28	3	3	285	64
Percent of total eggs	21	35	6	1	1	64	

spiracles, (fig. 5) and by the presence of anterior spiracles. The cephalopharyngeal skeleton (fig. 2) has well-demarcated mandibular, dental and hypostomal sclerites of characteristic shape, the mandibular and dental are slender at the point of articulation, and the tips of the mouthhooks are not articulated to the mandibular sclerite.

Third instar. The larger body (6.0 to 11.9 mm. in length) and longer cephalopharyngeal skeleton (1.45 mm. long, 0.48 mm. high) distinguish this instar. The cephalopharyngeal skeleton (fig. 3) has a very different appearance, with the hypostomal sclerite much shorter, the dental sclerite shorter, more massive in shape and more broadly articulated, and the tips of the mandibular sclerite apparently deeply cleft in lateral view. The posterior spiracles (fig. 6) have three slits and a definite button. Figure 7 shows the locomotor pads of the last two segments and the raised nature of the posterior spiracle. Figures 7, 8, and 9 show the posterior spiracles and four pair of anal lobes on the last segment.

Activity. The duration of each larval instar was not determined. The combined length of time in the egg and larval stages under laboratory conditions varied from 9 to 13 days with an average of 10.2 days (Table I). Since the greatest percentage of hatching was noted on the second day after oviposition (Table III), it is assumed that the length of the larval stage extends from 7 to 11 days, with an average of approximately 8 days.

Larval activity within the rearing media for the first 6 to 7 days of development was observed to occur in the outer 1½ inches of rearing mash in contact with the glass jar wall, and extending down 3 inches from the top of the mash. Temperature recordings, taken at the center of the

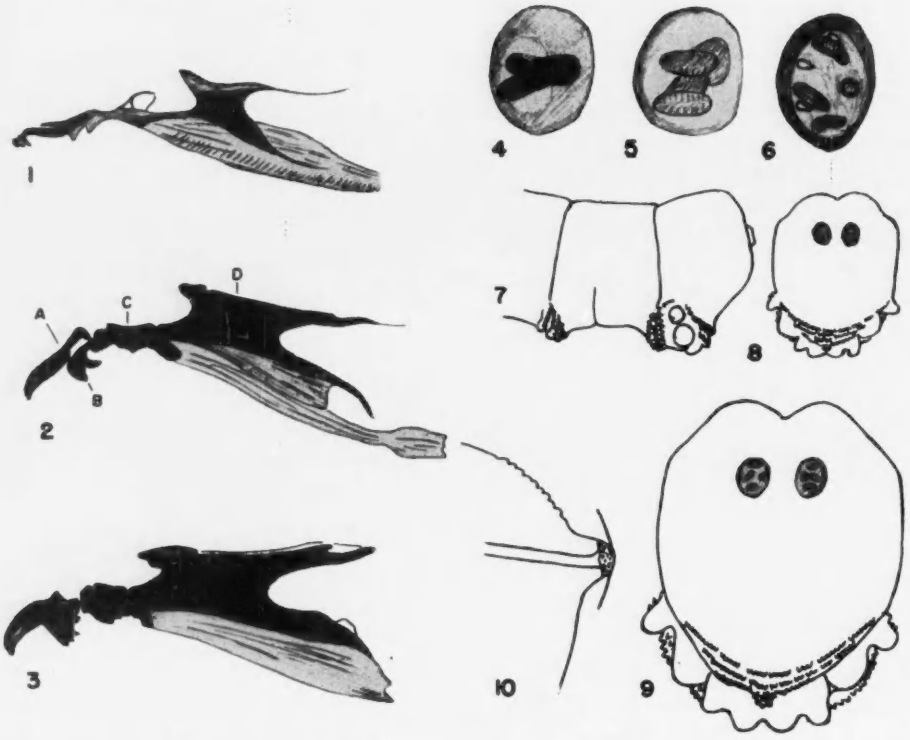

FIG. 1. Cephalopharnygeal skeleton, first instar larva.
FIG. 2. Cephalopharyngeal skelton, second instar larva sclerites as follows: (a) mandibular, (b) dental, (c) hypostomal, and (d) pharyngeal.
FIG. 3. Cephalopharyngeal skeleton, third instar larva.
FIG. 4. Left posterior spiracle, first instar larva.
FIG. 5. Left posterior spiracle, second instar larva.
FIG. 6. Left posterior spiracle, third instar larva.
FIG. 7. Posterior segments, lateral view, mature larva.
FIG. 8. Posterior view of mature larva.
FIG. 9. Posterior view of mature larva further enlarged.
FIG. 10. Sectional view through posterior spiracle, first instar larva, showing the dendritic hairs attached to the spiracle and the mammilate area dorsal to the spiracle.

rearing medium at 1, 2, 3, and 4 days after mixing, were 38° C., 36° C., 48° C., and 37° C., respectively. Temperatures within the mash dropped progressively from the third day until an equilibrium of approximately 31° C. was reached on the seventh day and maintained through the eleventh day.

No concise work was done to determine the maximum, minimum, or threshold temperatures of larval forms of this species. However variations of the malt extract and yeast content of the mash rearing media were made in attempts to shorten the length of the larval stage. The reduction of these constituents in the mash mixture did not markedly reduce mash fermentation, the temperature, or the length of the larval stage.

pupa, based on 2450 pupae weighed in lots of 25 each, was found to be 16.3 mg. The range in pupal weight as indicated by averages of the lightest and heaviest lots of 25 pupae was found to be 11.7 to 20.0 mg. per pupa.

Observations of puparial development of larvae removed from the rearing media and held at 80° F. and 70 percent relative humidity revealed that approximately 60 minutes were required between the first noticeable shortening and complete immobility. Progressive darkening of the puparium continued for an additional 5 hours.

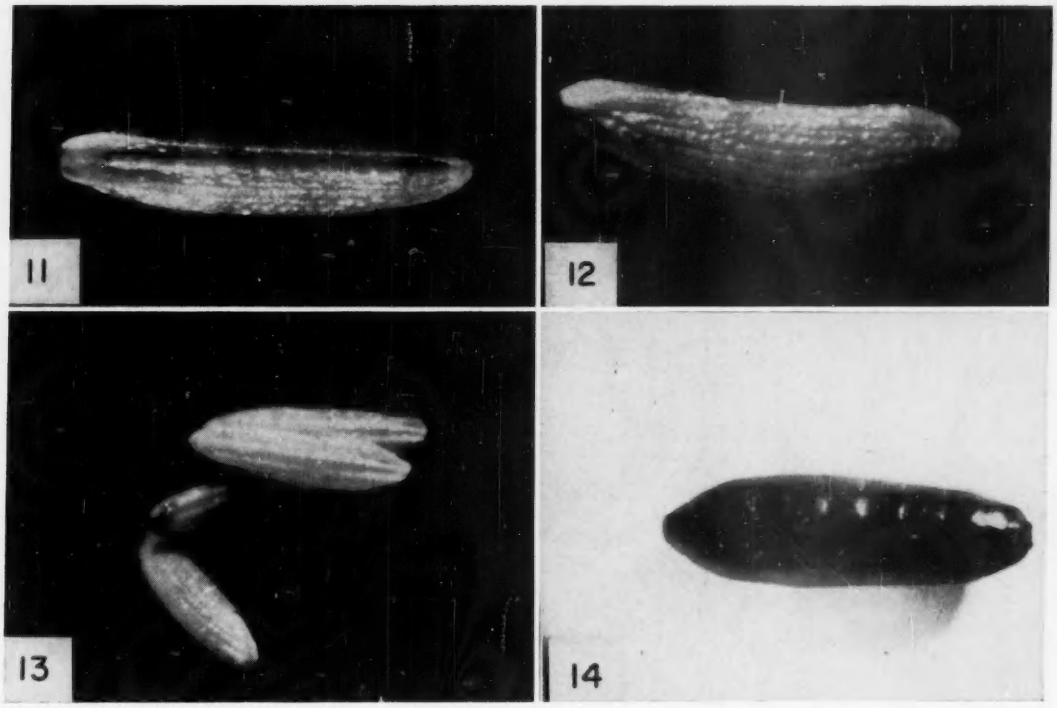

FIG. 11. Egg, dorsal view. FIG. 12. Egg, lateral view. FIG. 13. Group of eggs. FIG. 14. Puparium. (Figures 11–14, photographs by Mary S. Crawford)

THE PUPAL STAGE

Description of Puparium. The pupa is enclosed within a puparium (fig. 14) which is shorter and more oval than the larva. The small cephalic segment is retracted and the dark brown body of 11 apparent segments is 6.2 to 6.6 mm. long, bluntly rounded at both ends with the anterior end more tapering. The cuticula is rugulose about the posterior spiracles. The average weight per pupa, based on 2450 pupae weighed in lots of 25 each, was found to be 16.3 mg. The range in pupal weight as indicated by averages of the lightest and heaviest lots of 25 pupae was found to be 11.7 to 20.0 mg. per pupa.

Adults emerged from 55.5 percent of pupae weighing 17.1 mg. in a series of rearing jars set for colony maintenance (Table I). The length of the pupal stage estimated from group data (Table I) was 4 to 8 days with an average of 6.6 days.

In an effort to get larvae to leave the media prior to pupation, approximately 3 pints of dry, sifted sand was poured on media at 4, 5, 6 and 8 days after seeding. On the twelfth day the sand was sifted but in all series most pupae were either at the moist sand line or in the moist mash and it was necessary to pick these pupae by hand. Wet cheese cloth placed in lieu of the dry sand on the top of the medium on the eighth day did

not induce greater larval migration to the top surface for pupation than did the sanding methods.

THE ADULT STAGE

Description. The adult fly, previously known as D. *hilariformis* (Stein), has recently been carfeully described (Snyder, 1955). The following brief description should adequately distinguish adult *D. scabra* from other North American muscoid flies.

Slender, greyish flies, about as long as *Musca domestica* L. (5.0–7.2 mm.) but not as stout as that species. Perhaps the most distinctive feature is the generic character: the presence of an outwardly curved bristle on the lower cheek, somewhat laterad of the usual row of bristles which borders the buccal cavity. The arista is short plumose. The thorax is grey, with a median brownish stripe which does not reach the scutellum or the anterior margin. There are usually three posterior dorsocentral bristles (between the scutellum and the transverse suture of the mesonotum). The abdomen is uniformly grey in the female, and grey with a median darker stripe in the male. The fourth wing vein is continued straight to the wing margin, parallel to vein 3. The membrane of the wings often is slightly brownish, clouded along the veins. The legs are elongate, dark, or with the tibiae dark reddish.

An allied species *D. querceti* (Bouché) has usually four posterior dorsocentrals and is further distinguished by the median mesonotal stripe continued to the anterior margin of the thorax. This species may be confused macroscopically with *Hydrotae houghii* Malloch, rather than with *D. scabra*. It has been taken only once in privy trapping at Savannah, (Kilpatrick and Schoof, in M.S.) and has been reared from sludge in garbage cans in that city. (Quarterman et al., 1949).

Longevity: Of the 30 wild flies used to establish the colony in September, 1953, the last died in the laboratory colony cage 45 days after capture. Longevity of insectary-reared female flies ranged from 29 to 61 days with an average of 40 days. Male specimens died in less than 25 days. Of the eggs set, 41 percent ultimately emerged as adults with a sex ratio of 49 males to 51 females.

SUMMARY

Descriptions and developmental data are reported for the egg, larva, pupa, and adult stages of *Dendrophaonia scabra* (Giglio-Tos) when reared under insectary conditions of 80° F. and 70 percent relative humidity at Savannah, Georgia.

Of the materials tried, cow manure was the preferred oviposition medium with eggs being deposited in groups in the cracks and crevices of the excrement. The preoviposition period for adult females averaged 14 days and the greatest percentage of eggs hatched 48 hours after deposition. An average of 64 percent of the eggs hatched.

The larval stage consisted of three instars which could be distinguished by the structure of the cephalopharyngeal skeleton and the posterior spiracles. The length of the larval period was approximately 8 days. The larvae tended to pupate in the moist mash.

Pupal weight ranged from 11.7 to 20.0 mg. with the average duration of the pupal stage being 6.6 days. The adult female survived for an average of 40 days, and deposited about 230 eggs per specimen. The minimum life cycle of 80° F. and 70 percent relative humidity was approximately 29 days.

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Erratum

On page 402 of Volume 48 last word of fourth paragraph of the Summary should be causal instead of casual.

EFFECTS OF NATURAL TEMPERATURES ON OVIPOSITION OF VARIOUS NUMBERS OF AN INSECT PARASITE (HYMENOPTERA, CHALCIDIDAE, TENTHREDINIDAE)[1, 2]

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The number of progeny left by insect parasites is determined not so much by their potential egg production as by the number of host insects that they are able to find and parasitize. Two important factors affecting the number and distribution of parasite progeny are the density of the host population exposed to attack and the number, or density, of female parasites searching for suitable hosts. Though the role of host density in controlling the reproduction of a parasite population has received more attention, the effect of parasite density on the oviposition of a parasite population is also of importance in host-parasite interaction. At a given density of the host population, variation in the number of adult female parasites modifies the number of hosts attacked, the total number of parasite eggs laid, and the number of parasite eggs deposited in each host exposed to attack.

In the laboratory, the effect of parasite density on parasite oviposition was examined (Burnett, 1953) when various numbers, ranging from 2 to 64, of the chalcid parasite *Dahlbominus fuscipennis* (Zett.) searched for 25 cocoons of its host insect, *Neodiprion sertifer* (Geoff.), which were distributed uniformly over an area of 50 square inches. With increase in the number of parasites released in the experimental cages the number of hosts attacked increased rapidly at the lower densities but more slowly at the higher densities; the increase in the number of parasite eggs laid varied, very roughly, as the square root of parasite density; the number of eggs per parasitized host increased; and, usually, the rate of oviposition per female parasite decreased. Variation in temperature affected the ability of *D. fuscipennis* to parasitize hosts as well as the number of eggs laid at any parasite density.

In these laboratory experiments the parasites searched at constant temperatures of 16°, 20°, and 24° C. for hosts distributed in small, darkened cages. This type of environment is markedly different from that in which *D. fuscipennis* ordinarily reproduces, and it is therefore of interest whether the relationship between parasite density and oviposition obtained in the laboratory can be reproduced under more natural conditions. A situation intermediate between laboratory and field conditions is found by distributing cocoons on a grass lawn at a given density and releasing various numbers of adult female parasites among the hosts. Under these conditions the parasites are not confined to a restricted area, although their host insects are, and they are exposed to all the variations associated with weather but not those major discontinuities of the natural environment attributable to vegetation. In addition, the effect of variation in some physical factor such as temperature on the relation of parasite density and parasite oviposition can be used as an index of the role of climatic factors in this type of host-parasite interaction.

This paper deals with the relation of parasite density to parasite oviposition when various numbers of *D. fuscipennis* were released among a constant number of cocoons of *N. sertifer* distributed over small plots laid out on a grass lawn.

MATERIALS AND METHODS

The European pine sawfly *N. sertifer* is a pest, in Canada, of Scotch pine, *Pinus sylvestris* L. Mature sawfly larvae were collected in the field and allowed to form cocoons in cages and the cocoons were stored at 1° C. until required. Immediately before use on the experimental plots the cocoons were immersed in hot water to kill the host insect. *D. fuscipennis* pierces the cocoon of *N. sertifer* with its ovipositor, paralyzes the spun-up insect and deposits a considerable number of eggs on the surface of the host. The adult female parasites used in the experiments were propagated in the laboratory at 22° C.

At the beginning of each experiment six plots, five feet by five feet in area, were laid out on a grass lawn. One hundred cocoons of *N. sertifer* were distributed in a 10-by-10 pattern on each of the six plots. A different number of females of *D. fuscipennis* was released in the center of each of the six experimental plots. The parasites were released in groups of 12, 25, 50, 100, 200, and 400 when the plots were shaded from direct sunlight. The females were 24 to 48 hours old at the beginning of each experiment. The cocoons were collected 18 to 20 hours later and the number of eggs deposited on each host was recorded. Two series of six plots each were used alternately and the numbers of parasites released on each plot within each series were varied. Throughout the season it was possible to complete 14 replicates.

The maximum and minimum temperatures occurring during the 18 to 20 hours of each experi-

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[2]The assistance of Mr. G. Williamson, Entomology Laboratory, Belleville, is gratefully acknowledged.

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Date of acceptance, Nov. 10, 1954.

ment were recorded in a standard weather shelter adjacent to the experimental plots.

PARASITISM OF THE HOST

The average numbers of hosts parasitized by the six groups of *D. fuscipennis* when searching for 100 cocoons of *N. sertifer* distributed over 25 square feet of grass lawn are given in Table I. The average of the maximum and minimum temperatures recorded during each experiment was used as an indication of the temperatures occurring during the experiment. The 14 replicates were divided into two groups: five replicates had an average temperature below 17.5° C., and nine replicates had an average temperature between 17.5° and 24° C. The standard errors recorded in Table I, and also in Tables II and III, indicate the amount of variation in the results. At the lower parasite densities there was a rapid increase in the number of hosts found by the parasites as the number of parasites released was increased. With further increase in the number of female parasites released the numbers of additional hosts parasitized increased less rapidly. The number of hosts found by a given number of parasites was always greater at the higher temperature.

TABLE I

AVERAGE NUMBERS OF HOSTS PARASITIZED BY DIFFERENT NUMBERS OF FEMALES OF *D. fuscipennis* WHEN SEARCHING FOR 100 COCOONS OF *N. sertifer* DISTRIBUTED OVER 25 SQUARE FEET OF GRASS LAWN

NUMBER OF PARASITES LIBERATED	AVERAGE NUMBER OF HOSTS PARASITIZED			
	below 17.5° C.		17.5° –24° C.	
	Mean	Standard Error	Mean	Standard Error
12	3.4	0.748	5.1	0.611
25	9.2	0.583	11.3	1.040
50	13.8	1.428	19.0	2.624
100	23.4	1.122	27.8	3.054
200	30.4	5.971	40.1	4.188
400	37.0	2.664	50.4	3.488

The numbers of eggs deposited by various numbers of *D. fuscipennis* when searching for 100 cocoons of *N. sertifer* are given in Table II. With increase in the number of parasites liberated there was an increase in the number of eggs deposited at both the lower and upper temperature ranges. With increase in the number of females released, however, the parasites did not attack hosts at the same rate as they deposited eggs in the parasitized cocoons. The number of eggs laid by a given number of parasites was always greater at the higher temperature range.

Since the relation of parasites released to hosts parasitized (Table I) differed from that of parasites released to parasite eggs deposited (Table II), it follows that the number of parasite eggs per parasitized host varied as the number of parasites released was increased. In Table III the numbers of eggs per host attacked are recorded for both temperature ranges. The increase in eggs per host with increase in parasites liberated indicates that an increasing number of hosts were attacked by more than one parasite. In the propagation of *D. fuscipennis* on cocoons similar to those used in the experiments, the number of parasites reared on a single host was 20 to 30. Therefore, superparasitism at higher densities of parasites would lead to some mortality of the developing parasite larvae.

TABLE II

AVERAGE NUMBERS OF EGGS LAID BY DIFFERENT NUMBERS OF FEMALES OF *D. fuscipennis* WHEN SEARCHING FOR 100 COCOONS OF *N. sertifer* DISTRIBUTED OVER 25 SQUARE FEET OF GRASS LAWN

NUMBER OF PARASITES LIBERATED	AVERAGE NUMBER OF PARASITE EGGS LAID			
	below 17.5° C.		17.5° –24° C.	
	Mean	Standard Error	Mean	Standard Error
12	76.0	30.167	119.8	15.709
25	205.0	28.249	288.1	41.800
50	461.0	113.990	577.6	75.299
100	698.8	184.176	964.1	170.232
200	1044.0	373.555	1692.8	292.457
400	1559.8	339.103	2558.3	367.783

TABLE III

AVERAGE NUMBERS OF EGGS LAID IN EACH HOST PARASITIZED BY *D. fuscipennis*

NUMBER OF PARASITES LIBERATED	AVERAGE NUMBER OF PARASITE EGGS PER PARASITIZED HOST			
	below 17.5° C.		17.5° –24° C.	
	Mean	Standard Error	Mean	Standard Error
12	20.1	3.155	23.4	1.372
25	22.5	3.440	25.4	2.293
50	32.8	5.473	30.9	3.515
100	28.8	6.156	33.4	3.121
200	31.2	4.283	40.1	3.225
400	41.5	7.574	49.0	3.727

As the number of parasites released on each experimental plot was increased there was a change in the efficiency of the average female of *D. fuscipennis*. The average numbers of hosts parasitized by each parasite at the lower and upper temperature ranges are given in Table IV for each of the six groups of parasites released. With initial increase in parasites searching for 100 cocoons of *N. sertifer* the average female found more hosts at both the lower and upper temperature ranges. But with further increase in the

number of parasites released there was a rapid decline in the number of hosts attacked by each female. As is to be expected from Table I, for each group of parasites released there were more hosts parasitized at the higher than at the lower temperatures by a single parasite. The average numbers of eggs deposited by each parasite at the lower and upper temperature ranges are also given in Table IV for each parasite density. With the increase from 12 to 25 or 50 in the number of parasites searching for 100 cocoons the average female laid more eggs. But with further increase in parasite numbers there was a marked decline in the reproduction of each parasite. As is to be expected from Table II, the higher temperature range caused a higher rate of oviposition at each parasite density.

TABLE IV

RELATION OF PARASITISM TO NUMBERS OF FEMALE PARASITES LIBERATED

NUMBER OF PARASITES LIBERATED	HOSTS PARASITIZED PER FEMALE PARASITE		EGGS LAID PER FEMALE PARASITE	
	below 17.5° C.	17.5°–24° C.	below 17.5° C.	17.5°–24° C.
12	0.289	0.434	6.3	10.0
25	0.368	0.452	8.2	11.5
50	0.276	0.380	9.2	11.6
100	0.234	0.278	7.0	9.6
200	0.152	0.201	5.2	8.5
400	0.092	0.126	3.9	6.4

COMPARISON OF LABORATORY AND FIELD RESULTS

In the laboratory experiments (Burnett, 1953) 25 cocoons of *N. sertifer* were distributed uniformly in a 5-by-5 pattern over 50 square inches of damp moss. Eight numbers, *i.e.*, 2, 4, 9, 16, 25, 36, 49, and 64, of female parasites searched for hosts for 24 hours at constant temperatures of 16° and 20° C. In the experiments on the grass lawn 100 cocoons were distributed in a 10-by-10 pattern and six numbers, *i.e.*, 12, 25, 50, 100, 200, and 400, of female parasites searched for hosts for 18 to 20 hours at natural temperatures. The trend of the relation of parasitism to parasite density may be described only in some instances by a simple equation. Therefore, a comparison of the number of hosts parasitized and of the number of parasite eggs deposited was made graphically.

The increases in the number of hosts parasitized in the laboratory and outdoor experiments as the density, or number, of female parasites released was increased are compared in fig. 1. Since the numbers recorded in the laboratory and the lawn experiments were of different magnitudes, different scales were used for the two sets of results. In constructing fig. 1 the number of hosts parasitized at the highest parasite density and at a constant temperature of 20° C. in the laboratory experiments was made coincident with the greatest number of hosts parasitized when 400 females of *D. fuscipennis* were released and the average temperature range was 17.5°–24° C. in the experiments on the grass plots. The scales on the two abscissae and ordinates were determined by this point and the origin. Since the numbers of hosts parasitized at 16° C. in the laboratory and in the temperature range below 17.5° C. on the grass plots were plotted from the scales on the coordinates, the relative positions of the two curves were not predetermined. Fig. 1 shows that the trends in the number of hosts parasitized with increase in parasite density were approximately the same in

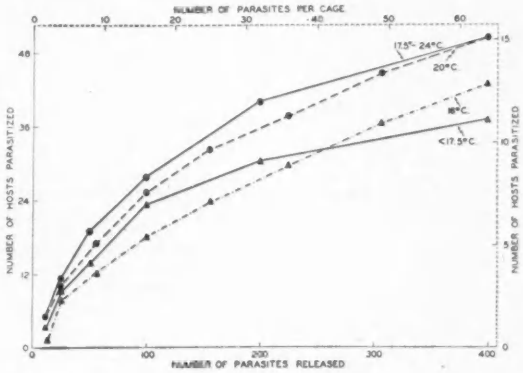

FIG. 1. Comparison of the trends in the number of *N. sertifer* parasitized with increase in parasite density in laboratory cages (broken lines; 2 to 64 parasites released among 25 hosts) and on 25-square-foot plots of grass lawn (solid lines; 12 to 400 parasites released among 100 hosts) by females of *D. fuscipennis* at various temperatures.

the laboratory experiments at 20° C. and in the outdoor experiments whose average temperatures were between 17.5° and 24° C. With a decrease in temperature from 20° to 16° C. in the laboratory and from a temperature range of 17.5°–24° C. to below 17.5° C. on the grass lawn, there was a slight differential response in the ability of *D. fuscipennis* to find hosts in the experimental cages and on the 25-square-foot plots; the parasites found relatively fewer hosts in the laboratory cages than on the grass plots at the lower parasite densities and relatively more at the higher densities.

The trends of the increase in the number of parasite eggs deposited in the laboratory and outdoor experiments as the number of female parasites released was increased are compared in fig. 2. The curves of fig. 2 were plotted in the same manner as for fig. 1. The trends in the oviposition of *D. fuscipennis* in the laboratory experiments at 20° C. and in the plot experiments

with a temperature range of 17.5°–24° C. were almost identical. At most parasite densities used in these experiments a temperature drop from 20° to 16° C. in the laboratory and from a range of 17.5°–24° C. to a range below 17.5°C. on the grass lawn produced the same relative effect on parasite oviposition.

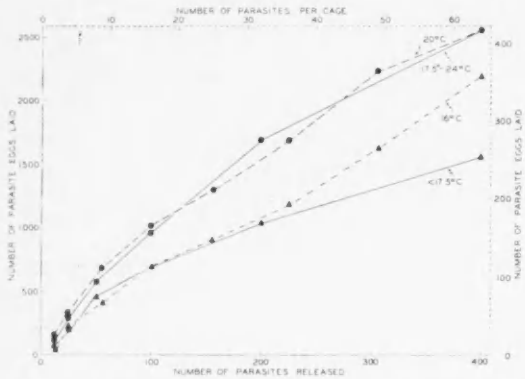

FIG. 2. Comparison of the trends of the number of parasite eggs deposited with increase in parasite density in laboratory cages (broken lines; 2 to 64 parasites released among 25 hosts) and on 25-square-foot plots of grass lawn (solid lines; 12 to 400 parasites released among among 100 hosts) by females of *D. fuscipennis* at various temperatures.

DISCUSSION

It is unlikely that the ability of *D. fuscipennis* to find and parasitize cocoons of *N. sertifer* remains unchanged when the searching for hosts is transferred from the laboratory to the field. Several factors were observed that acted on the parasites released on the grass plots but not on those used in the laboratory. On the lawn, approximately one percent of the host cocoons were destroyed by birds. The oviposition of the parasite was decreased very greatly by rain and heavy dew and therefore the experiments subjected to rain were discarded. The parasites tended to disperse in one direction and the dispersion was affected by the direction and strength of the wind. Finally, variation in the density of grass within a plot modified the rate of dispersion.

The effect of temperature on the relation between parasite density and parasite oviposition was used as an example of the influence of physical factors on density-dependent processes. The average of the maximum and minimum temperatures during each experiment was used as a measure of temperature because on this basis the series of replicates could be separated into three distinct groups. Since only one experiment had an average temperature above 24° C. this result was discarded. It is realized that the two temperature ranges (below 17.5° C. and 17.5°–24° C.) are not strictly comparable to constant temperatures of 16° and 20° C. The number of experiments occurring within each temperature range and the total number of experiments conducted during the season were, of course, dependent on the weather conditions.

In spite of the many contrasts apparent between the laboratory and lawn experiments, the agreement between the trends in parasitism with increasing parasite density for the two sets of results is remarkably close.The rates of increase in the number of hosts parasitized in the laboratory experiments at 16° C. and in the lawn experiments that had average temperatures between 17.5° and 24° C. were much the same. At the lower temperatures in the two environments the rates at which *D. fuscipennis* found hosts, as parasite density was increased, were somewhat different but the general trend in the laboratory was similar to that on the grass plots. The variation in the number of eggs laid by the parasites was much the same, at comparable temperatures, in the two sets of experiments. This general similarity in trends of parasitism was strengthened, no doubt, because each female parasite attacked only one host and laid many eggs in the parasitized cocoon rather than depositing one egg in each host and searching for many hosts. An increase in temperature resulted in more hosts being parasitized and more eggs being deposited in each cocoon on both laboratory and field studies. It is remarkable that the parasitism of the host in the laboratory and on the grass plots decreased by much the same relative amount with decrease in temperature. In general, there was an optimum number of parasites released, in both the laboratory cages and on the grass plots, for the efficiency of the individual female of *D. fuscipennis* in finding hosts and depositing eggs. With the initial increase in parasite density more hosts were parasitized and more eggs deposited by the average parasite. At the higher parasite densities there was a marked decline in parasitism by individual females. This change in the searching ability of female parasites was more pronounced in the field experiments than in the laboratory studies.

Variation in parasite density influenced the oviposition of *D. fuscipennis* in a similar manner when the parasite was confined to small, darkened cages and when it was released among sawfly cocoons distributed over plots of a grass lawn. Variation in temperature also tended to produce the same effect in the reproduction of the parasite in the laboratory and in the semi-natural environment employed in the lawn experiments. It seems likely, therefore, that the pattern of searching by females of *D. fuscipennis* in the laboratory experiments was typical of what occurs in a relatively uniform and limited natural environment. The host-parasite system

of the sawfly cocoon and *D. fuscipennis* appears to be satisfactory for analyzing the effect of parasite density on the oviposition of an insect parasite when the population of the parasite is exposed to both the minor and major discontinuities encountered in a natural environment.

SUMMARY

1. The effects of natural temperatures and parasite density on the oviposition of an insect parasite were examined when various numbers of *D. fuscipennis* were released among 100 cocoons of *N. sertifer* distributed in a 10-by-10 pattern on 25-square-foot plots of grass lawn.

2. The number of hosts parasitized and the number of parasite eggs deposited increased rapidly with initial increase in the number of parasites released. With further increase in parasites the parasitism increased more slowly.

3. There was an increase in superparasitism with increase in the number of parasites released.

4. There was an optimum density of adult parasites for maximum parasitism by the average female of *D. fuscipennis*.

5. As the temperature was increased the number of hosts parasitized and the number of eggs laid by a given number of parasites increased.

6. There was a reasonably close agreement between the relations of parasitism to parasite density in the laboratory and lawn experiments.

REFERENCE CITED

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COMPARATIVE STUDIES OF URBAN FLY POPULATIONS IN ARIZONA, KANSAS, MICHIGAN, NEW YORK, AND WEST VIRGINIA II. SEASONAL ABUNDANCE OF MINOR SPECIES[1]

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In a previous paper, (Schoof and Savage, 1955), the occurrence and seasonal distribution of the major species of flies recovered in trap surveys at Cohoes, New York; Grand Haven, Michigan; Dunbar-St. Albans, West Virginia; Lawrence, Kansas; and Mesa-Tempe, Arizona, during 1949 and 1950 were described. The present data are a sequel to that paper and treat the species of flies which were of minor significance in the over-all fly population of those communities. Reference to remaining species of flies trapped during the survey is limited to the check list of species for each city.[2]

METHODS

Details of the techniques used were described in the previous paper. In brief, the modified USDA fly trap (Coffey, 1948), was used to collect the flies, employing an attrahent of decaying fruit, vegetables, and chicken viscera or fish. Collections were made on a weekly schedule in the various parts of the city, each trap operating for a single 24-hour period.

RESULTS

CALLIPHORIDAE

Five blow flies, *Bufolucilia silvarum*, *Calliphora vicina*, *Cynomyopsis cadaverina*, *Lucilia illustris*, and *Protophormia terrae-novae* frequented traps at all survey cities except Mesa-Tempe, Arizona. A sixth species, *Calliphora vomitoria*, occurred only at the New York, Michigan, and West Virginia cities.

Bufolucilia silvarum attained its greatest abundance at Grand Haven, Michigan, where it accounted for 1.0 and 2.5 percent of the total flies trapped during 1949 and 1950. This species occurred from May to October and averaged 44.4 and 84.1 flies per collection in 1949 and 1950. During the latter year, a total of 4,624 specimens was recovered from trap collections. In both 1949 and 1950, the peak densities occurred in July after which a gradual decline ensued.

At Cohoes, New York, and Dunbar-St. Albans, West Virginia, *B. silvarum* was collected from May through October. The maximum densities occurred in July and August at Cohoes, New York, and in June and August at Dunbar-St. Albans, West Virginia. At Lawrence, Kansas,

[1]Accepted for publication October 29, 1953.

[2]Check lists include those data obtained in trap surveys at Troy and Cohoes, New York (1948–50); Muskegon and Grand Haven, Michigan (1948–50); Topeka and Lawrence, Kansas (1948–50); Charleston, Dunbar, and St. Albans, West Virginia (1948–52); Phoenix, Mesa, and Tempe, Arizona (1948–52).

this species was captured infrequently; only seven specimens were recovered in 1949 (June) and 15 in 1950 (June).

Lucilia illustris was the only species classified as minor which accounted for more than 2.6 percent of the total flies trapped at any city during a single season. This species occurred in the greatest numbers at Grand Haven, Michigan, during 1950 (figure 1) when it represented 8.2 percent of the total flies collected. *L. illustris* was on the wing from May through October with peak densities in August 1949 and July 1950. Yearly indices were 148.8 and 272.7 specimens per collection for 1949 and 1950, respectively.

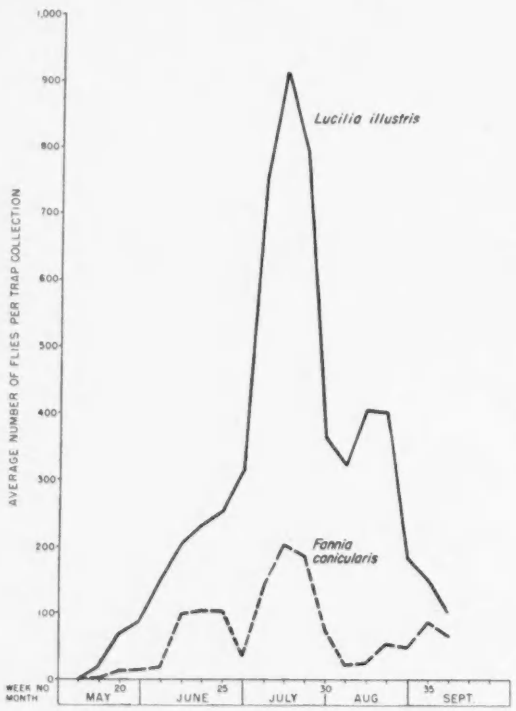

FIGURE 1. Seasonal prevalence of *Lucilia illustris* and *Fannia canicularis* at Grand Haven, Michigan (May–September, 1950).

At Cohoes, New York, *L. illustris* averaged 50.0 and 14.4 flies per collection in 1949 and 1950. During the former year, it attained a June peak of 130 flies per collection; in 1950, the maximum index of 40 flies occurred in August. At Dunbar-St. Albans, West Virginia, the average indices for *L. illustris* during 1949 and 1950 were only 12.1 and 13.7 flies per collection; however, this species prevailed from April to November. Peak density occurred in June during both years. At Lawrence, Kansas, only 12 specimens of *L. illustris* were trapped during 1949, these flies being recovered from a single collection in June. No flies of this species were collected in 1950.

Despite the occurrence of the blue bottle flies, *Calliphora vicina* and *Cynomyopsis cadaverina*,[3] in collections from all cities except Mesa-Tempe, Arizona, neither species accounted for more than 1.0 percent of the flies trapped in a single season. *C. cadaverina* attained its greatest density at Cohoes, New York, in 1949 when 2059 specimens were captured for an average of 23.1 flies per collection. However, the 1950 population was greatly reduced with only 109 specimens recovered. The prevalence trends for *C. cadaverina* were similar at all cities. After an April-May peak, the species disappeared from collections in July and August.[4] In fall it reappeared, displaying a secondary peak during the October-November period.

Calliphora vicina was absent in Mesa-Tempe, Arizona, but occurred throughout the surveys at the remaining cities. This species never occurred in numbers, the maximum index occurring at Dunbar-St. Albans, West Virginia, in 1950 when 875 specimens were recovered. *C. vicina* reached May maxima of 37.3 and 22.2 flies per collection during 1949 and 1950, respectively, at this city. After mid-June, it remained at stable levels of less than 9 flies per collection. This species was only of minor occurrence (98 to 463 flies per season) at Cohoes, New York; Grand Haven, Michigan; and Lawrence, Kansas.

Calliphora vomitoria was not recovered in Mesa-Tempe, Arizona, or Lawrence, Kansas,[5] and was relatively scarce at the other three cities, the largest number collected being 743 specimens at Cohoes, New York, during 1949 for an average of 8.3 specimens per collection. The prevalence trend of *C. vomitoria* at this city in 1949 is depicted in figure 2. In 1950, however, only three specimens were recovered.[6] At Grand Haven, Michigan, trap collections produced 73 and 93 specimens of *C. vomitoria* during 1949 and 1950, the species being on the wing from May through October. *C. vomitoria* was rarely taken in Dunbar-St. Albans, West Virginia, collections (17 specimens, 1949; 29 specimens, 1950), the positive collections occurring in the spring or in October.

Protophormia terrae-novae was most abundant in Cohoes, New York, in 1949 when 1733 specimens were recovered for an average of 19.5

[3] *Calliphora vicina* was not found in the Mesa-Tempe collections; however, two specimens were collected at nearby Phoenix, Arizona, in 1951 (one in April and one in May).

[4] Thirty-eight specimens were recovered from a single collection during an abnormally wet and cool July in 1950 at Lawrence, Kansas.

[5] One specimen of *C. vomitoria* was collected at nearby Topeka, Kansas, November, 1948; two specimens at Phoenix, Arizona, November, 1949.

[6] In 1950, no collections were made in October, a factor which contributed to this marked reduction since cool weather favored this species (figure 2).

flies per collection. However, in the 1950 trap collections, only two specimens of *P. terrae-novae* were recovered at this city. During 1949, *P. terra-novae* occurred from May through October, with a peak in July. At Grand Haven, Michigan, an average per collection of 21.4 and 2.5 specimens was trapped during 1949 and 1950, respectively. In 1949, this species was collected from June through September; in 1950, from May through August. Peak densities during both years were attained in July. At St. Albans, West Virginia, only 12 specimens of *P. terrae-novae* were collected during the survey; all were caught in a single July collection during 1949.

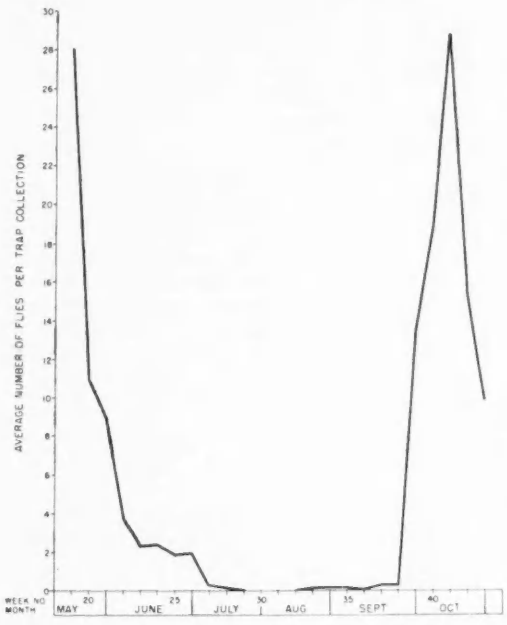

FIGURE 2.—Seasonal prevalence of *Calliphora vomitoria* at Cohoes, New York (May-October, 1949).

OTITIDAE

Chrysomyza demandata (figure 3) attained its greatest prevalence at Mesa-Tempe, during 1950 when 4949 specimens were recovered for an average of 32.6 specimens per collection; during 1949, 1256 specimens averaged 9.2 flies per collection. In this area, *C. demandata* showed peak densities in June, appearing in collections from March through December 1949; and from April through November 1950. This species was much less abundant at the remaining cities, average densities for 1949 and 1950 being 2.0 and 0.4 respectively at Lawrence, Kansas; 1.3 and 0.6 at St. Albans-Dunbar, West Virginia; 4.1 and 0.3 at Grand Haven, Michigan; and 1.6 and <0.1 at Cohoes, New York. In general, *C. demandata* exhibited maximum densities in these cities during the summer period.

Euxesta notata did not occur at Mesa-Tempe, Arizona,[7] but was present in the remaining cities being collected in greatest numbers at Grand Haven, Michigan, in 1949 when 450 specimens were recovered (16.7 flies per collection). In 1950, 150 specimens were collected in this same city. At the New York, Kansas, and West Virginia cities, *E. notata* was less abundant, being least prevalent at Cohoes, New York, where the total number of specimens obtained in 1949 and 1950 was 31. In all cities, the species was on the wing throughout the fly season.

MUSCIDAE

Hydrotaea houghii appeared in trap collections in all cities except Mesa-Tempe, Arizona. This species appeared most frequently in the 1950 collections from Grand Haven, Michigan, where

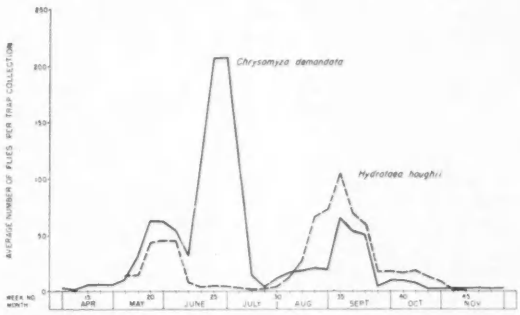

FIGURE 3. Seasonal prevalence of *Chrysomyza demandata* at Mesa-Tempe, Arizona (March–November, 1950), and *Hydrotaea houghii* at Dunbar-St.Albans, West Virginia (May-November, 1950).

it averaged 54.2 flies per trap collection. In 1949, the average index was 18.3 flies per collection. Peak densities occurred in July 1949 and June 1950.

At Cohoes, New York, *H. houghii* averaged 10.4 and 2.2. flies per collection during 1949 and 1950, respectively, and was on the wing from May through October. In 1949, it reached maximum prevalence in June. In Dunbar-St. Albans, West Virginia, 299 and 3251 specimens of *H. houghii* were collected in 1949 and 1950. The incidence curve of this species at Dunbar-St. Albans, West Virginia, during the latter year is depicted in figure 3. In contrast to the May and September maxima in 1950, a single June peak occurred in 1949. At Lawrence, Kansas, *H. houghii* was present from April to November, reaching maximum prevalence in July, 1949 and in June, 1950. During the former year, *H.*

[7]One specimen of *E. notata* was collected at Phoenix, Arizona, September, 1949.

houghii averaged 4.7 flies per collection; in 1950, 4.3 flies per collection.

Several species of the genus *Fannia* occurred in collections from all survey cities. The most abundant species collected in the five cities was the little house fly, *Fannia canicularis;* however, it never accounted for more than 1.8 percent of the total flies trapped in any city during a single season. *F. canicularis* was most plentiful at Grand Haven, Michigan, where it represented 0.4 and 1.8 percent of the total flies trapped in 1949 and 1950 and yielded indices of 18.7 and 61.3 specimens, respectively. The prevalence trend for 1950 is depicted in figure 1.

Average indices per trap collection for Cohoes, New York, were 8.7 and 4.1 in 1949 and 1950, respectively; for Dunbar-St. Albans, 3.6 and 10.2, and for Mesa-Tempe, Arizona, 2.2 and 1.3. *F. canicularis* displayed only meager prevalences at Topeka, Kansas; in 1949, only 14 specimens were retrieved; in 1950, the seasonal density increased to 108 specimens.

In all cities, numerous species were trapped in numbers too low to warrant individual discussion. Consequently, to provide an indication of the species spread at each location as well as distribution information on the different flies in relation to the five geographic areas, tabular lists of all species belonging to the families: Calliphoridae, Muscidae, Otitidae, Piophilidae, Sarcophagidae, Sepsidae, Stratiomyidae, Syrphidae, Sylvicolidae, and their months of recovery are given in table 1. Family lists of all other specimens collected during the survey are also shown. As this table shows, the number of individual species and families collected was greatest at Charleston and Dunbar-St. Albans, West Virginia (106 species in the nine prevalent families and representatives of 17 families of minor importance). Similarly, the number of species and flies determined only to family recovered at the remaining sites were: 103 species and 10 families, Topeka and Lawrence, Kansas; 96 species, 10 families, Muskegon and Grand Haven, Michigan; 92 species, 11 families, Troy and Cohoes, New York; and 79 species, 11 families, Phoenix and Mesa-Tempe, Arizona. The rank of the last named communities is surprising in view of the prolonged fly season in the Arizona area which is 2 to 2½ times longer than that of any of the other municipalities.

The greatest variation in number of species present in any community occurred in the Muscidae. In the three northern areas, 49, 41 and 40 species of this family were recorded while the collections at Kansas and Arizona communities yielded 37 and 32 species, respectively. In contrast, the number of species of blow flies trapped was evenly distributed, the West Virginia area reporting 16 species, the Arizona area 12, the Kansas area 15, the New York area 13, and the Michigan area 14 species each.

DISCUSSION

The data presented in this paper coupled with those related to the major species (Schoof and Savage, 1955) provide a generalized index to the species which occur in these geographic areas and which are attracted to baited traps. Although the bait employed was a composite type, nonetheless it must be recognized that the capture of certain elements of the fly population was favored over others. For example, the absence of animal excrement as an ingredient would decrease the number of Sarcophagidae enticed into the trap. However, it is likewise apparent that similar handicaps would exist with almost any type of bait utilized. To an undetermined extent, the handicap inherent in the use of baited traps was overcome by employing the same types of mixed baits in the five cities. This fact, plus the magnitude of the trapping and the tenure of the studies lends substantial weight to the comparative data presented.

The relative importance of blow flies and house flies in urban fly populations has been shown to vary in accordance with the geographic location. It is interesting to note that while the relative prevalence of blow flies in Phoenix, Arizona, is much lower than that of remaining cities, the number of blow fly species in each city remains essentially uniform. Species which occur more frequently in cooler climates, such as *Lucilia illustris*, *Bufolucilia silvarum*, and *Cynomyopsis cadaverina*, are absent in the hot, arid climate of the Arizona communities. In comparison, other species (*e.g.*, *Aldrichina grahami*, *Phaenicia mexicana*, and *Acronesia* spp.) which are indigenous to the Arizona communities do not occur in the northern cities.

As the data indicate, *Bufolucilia silvarum* was of common occurrence in trap collections from the northern projects. At Grand Haven, Michigan, the yearly index for 1950 was 84 specimens per collection. These findings agree with those of Dicke and Eastwood (1952) but are contrary to the statement by Hall (1948) that adults of this species are not often attracted to meat baits or collected from decaying substances.

With reference to the observed tendencies of *Cynomyopsis cadaverina* to show a marked decline in number or sometimes disappear during the warm summer months, there is evidence that this species survives as a semitorpid adult in cool, shaded locations. At Topeka, Kansas, during July, 1949, numerous adults of *C. cadaverina* were observed dispersed throughout the basement of a middle class residence. The basement was dark and damp, with only a few light rays filtering through four small windows. The owner complained that the flies had been annoying him for several days. An outside doorway to the basement presumably provided the means whereby the flies had gained entrance.

TABLE I

LIST OF THE SPECIES OF FLIES AND THEIR SEASONAL OCCURRENCE IN FIVE AREAS IN UNITED STATES AS REFLECTED BY TRAP COLLECTIONS*

CALLIPHORIDAE:	
Acronesia spp.	P(11, 12)**
Aldrichina grahami (Ald.)	P(2–6, 10–12)***
Bufolucilia silvarum (Mg.)	To(5–10); C(4–11); M(5–10); Tr(5–10)
Calliphora coloradensis Hough	P(1–6, 10–12); To(3, 5–7, 9, 10)
C. livida Hall	P(3–8, 10–12); To(3–5, 9, 10); C(4–6, 10); M(5–10); Tr(5, 6, 10, 11)
C. terrae-novae Macq.	P(1–5, 11, 12); To(3–5, 10, 11); C(3–5, 8, 10, 11); M(5, 6, 8–10); Tr(5, 6, 8–10)
C. vicina R.-D.	To (4–12); C(1–12); M(5–10); Tr(5–12)
C. vomitoria (L.)	P(11); To(11); C(1–5, 7–12); M(5–10); Tr(5, 6, 9–11)
Callitroga macellaria (F.)	P(1–12); To(4–11); C(4–11); M(6–10); Tr(5, 8–12)
Cynomyopsis cadaverina (R.-D.)	To(2–6, 8–12); C(1–5, 7–12); M(4–10); Tr(5–7, 9–11)
Eucalliphora lilaea (Walk.)	P(1–6, 9–12); To(5, 6); C(5, 6, 9, 10);
Lucilia illustris (Mg.)	To(4–7, 10); C(4–12); M(5–10); Tr(5–11)
Phaenicia caeruleiviridis (Macq.)	To(5–11); C(4–12); M(5–10); Tr(5–10)
P. cluvia (Walk.)	C(8);
P. mexicana (Macq.)	P(1, 3–12)
P. pallescens (Shan.)	P(1–12); To(4–11); C(4–12); M(8)
P. sericata (Mg.)	P(1–12; To (4–11); C(2–12); M(5–10); Tr(1, 5–12)
Phormia regina (Mg.)	P(1–12); To(3–11); C(2–12); M(5–10); Tr(5–11)
Protophormia terrae-novae (R.-D.)	C(5–7); M(5–10); Tr(5–11)
Pollenia rudis (F.)	To(2–10); C(1–12); M(6–8, 10); Tr (5–11)
MUSCIDAE:	
Anthomyia oculifera (Big.)	C(10)
A. pluvialis (L.)	P(3); To(6, 7, 9, 10); C(5–11); M(6–8); Tr(5, 6, 8–11)
Atherigona orientalis (Schiner)	P(7)
Calythea sp.	P(4–6)
Coenosia spp.	P(2–6, 9–12); To(3–10); C(4–11); M(5–8, 10); Tr(7–9)
Cryptolucilia caesarion (Mg.)	To(2–6, 9–11); C(7, 9); Tr(11, 12)
Dendrophaonia hilaraformis (St.)	To(8–11); C(8, 10, 11); Tr(9)
D. querceti (Bou.)	C(5, 9)
D. sp.	P(10); M(8);
Euryomma peregrinum (Mg.)	P(6, 11); To(6, 8, 9); C(5–11); M(6, 8, 9); Tr (8, 9)
Fannia americana Mall.	C(4, 5, 8, 9); M(6–10); Tr(6, 8)
F. canicularis (L.)	P(1–7, 9–12); To(3–11); C(2–12); M(5–10); Tr(5–11)
F. difficilis (St.)	C(4, 6, 8)
F. femoralis (St.)	P(3–12); To(6, 7); C(6, 7); M(7–9)
F. flavipalpis St.	P(3–7, 10, 11);
F. fuscula (Fall.)	C(6); M(7, 9); Tr(7, 8)
F. glaucescens (Zett.)	Tr(8)
F. howardi Mall.	To(6); C(5, 6, 8, 9);
F. laevis St.	P(2–7, 9–12)
F. leucosticta (Mg.)	C(5, 8–10); M(6–8); Tr(5)
F. manicata (Mg.)	M(5, 6, 8–10)
F. pellucida (St.)	C(8–10); Tr(8–10)
F. "pusio group"	P(1–12); To(5–7, 9, 10); C(4–10); M(5–9); Tr(5, 6, 8–10)
F. scalaris (F.)	P(3, 4, 7, 11); To(5–7, 9–11); C(4–11); M(5–10); Tr(5–11)
F. spp.	M(4, 7, 9, 10)
Fucellia maritima (Hal.)	C(3, 4, 10); M(5); Tr(1, 8–10)
Graphomya maculata (Scop.)	P(1-6, 10–12); To(5–10); C(4–10); M(6–9); Tr(5–9)
Hammonmyia paludis (Joh.)	C(4)
Hebecnema umbratica (Mg.)	C(4, 9); M(8)
Helina rufitibia (St.)	To(3, 4, 8–11); C(4, 5, 8, 9);
H. spp.	P(5, 10); M(5, 10); Tr(5, 8)
Hydrophoria spp.	Tr(11)
Hydrotaea occulta (Mg.)	P(3–5, 11, 12); To(3–7, 9, 10); C(2–10); M(5–10); Tr(1, 5–10)
H. armipes (Fall.)	M(7)
H. houghii (Mall.)	To(3–11); C(3–11); M(5–10); Tr(5–11)
H. spp.	C(6); M(7)
H. tuberculata (Ron.)	C(10)
Hylemya cilicrura (Ron.)	P(1–7, 10–12); To(3–11); C(2–12); M(5–10); Tr(5–11)
H. spp.	M(6–10)
Limnophora arcuata (St.)	P(1–8, 10–12); To(3, 5–11); C(2–11); M(5–9); Tr(5, 7–9)
L. cilifera (Mall.)	P(5); To(6, 7, 9, 10); C(5, 8–10); M(7); Tr(8)
L. debilis Will.	To(4)
L. narona (Walk.)	To(6–10); C(6–9); M(6–9); Tr(8)
Lipsa albitarsis St.	To(7, 9)
L. nasoni St.	To(9)
L. spp.	C(6); M(7, 10);
Morellia micans (Macq.)	To(5, 6, 9, 10); C(6–9); Tr(5, 6)
Musca domestica (L.)	P(1–12); To(4–12); C(4–12); M(5–10); Tr(5–11)
Muscina assimilis (Fall.)	P(1–12); To(4–11); C(1–11); M(5–10); Tr(5–11)

TABLE I—(Continued)

MUSCIDAE—(Continued)

M. aurantiaca Hough	P(3, 5, 9)
M. pabulorum (Fall.)	P(4, 9, 12); C(1, 3, 6, 9); Tr(5–10)
M. stabulans (Fall.)	P(1–12); To(3–11); C(2–11); M(5–10); Tr(5–11)
Mydaea spp.	C(4, 8, 9, 11)
Myospila meditabunda (F.)	P(4–7); To(4–11); C(1, 4–11); M(5–8, 10); Tr(5–11)
Ophyra aenescens (Wied.)	P(1–12); To(5–11); C(4–12); M(5–10); Tr(5–11)
O. leucostoma (Wied.)	To(5–11); C(2–11); M(5–10); Tr(5–11)
Pararicia pascuorum (Macq.)	To(9, 10); C(4, 7–11); M(7–10); Tr(5, 6, 8–11)
Paregle cinerella (Fall.)	P(1–7, 10–12); To(3–11); C(3–11); M(5–10); Tr(5–10)
P. radicum (L.)	M(5–8); Tr(5–10)
Pegomya spp.	P(4, 10–12); To(5–10); C(4–10); M(5–9); Tr(5, 8, 9)
Phaonia spp.	P(4, 6, 11, 12); To(6, 7, 9, 10); C(5, 9); Tr(5, 7, 10)
Pyrellia cyanicolor (Zett.)	To(4, 6, 9, 10); C(4, 5, 8, 10, 11); M(6, 7); Tr(5, 7–10)
Scopeuma furcatum (Say)	P(12); To(2–5, 8, 10, 11); C(1–6, 10–12); M(4–6, 9–10); Tr(5, 10, 11)
S. stercorarium (L.)	P(2–5); To(10); C(2–5, 7–12); M(5, 7, 10); Tr(1, 5, 6, 8–12)
Stomoxys calcitrans (L.)	P(7); To(7–10); C(7–10); M(6–10); Tr(8–10)
Synthesiomyia nudiseta (V. d. W.)	P(3–12); To(5–9); C(6, 8)

SARCOPHAGIDAE:

Eumacronychra spp.	P(4–6, 10, 11);
Hypopelta scrofa Ald.	To(7, 9, 10); C(4–11);
Macronichia aurata (Coq.)	Tr(6–9)
Sarcophaga aculeata Ald.	To(9)
S. alcedo Ald.	To(5, 6, 8–10); C(5, 7–10). M(6, 7); Tr(8, 10)
S. argyrostoma, R.D.	P(5–11); To(5–9); C(5–9); M(5–9); Tr(5–9)
S. atlanis Ald.	Tr(8)
S. aurea (Tns.)	P(3–12)
S. basalis Walk.	C(5, 8, 11)
S. bishoppi Ald.	P(3–11)
S. bullata Park.	To(4–10); M(5–10); Tr(5–10)
S. caridei Brethes	To(6); Tr(1, 5–10)
S. cessator Ald.	P(3)
S. cimbicis Tns.	To(4-7, 9–10); C(4–11); M(5–10); Tr(1, 5–10)
S. cingarus Ald.	To(7, 8, 10); C(4–10); M(6–10); Tr(6–10)
S. coolyei Park.	P(9–11)
S. crassipalpis Macq.	To(5–10); C(4–11); M(6–8); Tr(5–9)
S. duplicata Hall	P(4–11)
S. effrenata Walk.	P(3–12)
S. errabunda V. d. W.	P(3–12); To(6, 8, 9)
S. exuberans Pand.	To(8, 9)
S. falciformis Ald.	To(9)
S. galeata Ald.	To(5–10); C(4–11); M(6–10); Tr(8)
S. haemorrhoidalis Fall.	P(1, 3–12); To(4–11); C(4–11); M(5–10); Tr(5–11)
S. harpax Pand.	P(6); To(8); M(6)
S. houghii Ald.	C(5)
S. hunteri Hough	To(6, 9, 10); C(6, 7, 9); M(6, 7)
S. impar Ald.	To(4–11); C(4–8, 10); M(5–8); Tr(5, 9)
S. importuna Walk.	To(9); M(5–10); Tr(5, 8, 9)
S. kellyi Ald.	P(6); To(5, 6, 9, 10);
S. laakei Hall	P(2–12); To(5–10); C(4–11); M(6–8); Tr(5–10)
S. latisetosa (Park.)	To(5–10); C(3–11); M(5–10); Tr(6–10)
S. latisterna (Park.)	To(5, 6, 9, 10); C(6, 7, 9, 10); M(5–7, 9, 10); Tr(6)
S. lherminieri R. D.	P(1–12); To(4–11); C(4–11); M(5–10); Tr(5–10)
S. melampyga Ald.	C(5, 7–9)
S. melanura Mg.	C(6); Tr(5–10);
S. nearctica Park.	C(5, 7–10); M(5–10); Tr(5–10)
S. ochripyga V. d. W.	P(3–12)
S. opifera Coq.	To(9, 10)
S. pectinata Ald.	To(6); C(7, 8); M(7); Tr(7, 8)
S. planifrons Ald.	To(6–10);
S. plinthopyga Wied.	P(2–12);
S. polistensis Hall	P(9–11)
S. pusiola V. d. W.	To(5–11); C(4–11); M(5–10); Tr(5–11)
S. rapax Walk.	P(2–12); To(4–10); C(4–11); M(5–10); Tr(5–11)
S. reversa Ald.	To(7)
S. rudis Ald.	To(6)
S. sarracenioides Ald.	P(2–12); To(5–10); C(4–10); M(6–10); Tr(6, 8, 9)
S. servilis Ald.	To(7)
S. sinuata Mg.	To(4–6,9); C(3–7, 10, 11); M(5–9); Tr(5–9)
S. stimulans Walk.	To(5–10); C(4–11); M(6–10); Tr(7–11)
S. ochracea Ald.	P(1–12); To(5–11); C(4–11); Tr(6)
S. sulculata Ald.	P(3–12);
S. utilis Ald.	To(5–11); C(4–10); M(5–9); Tr(5, 7–8)

TABLE I—(Continued)

SARCOPHAGIDAE—(Continued):	
S. ventricosa V. d. W.	To(5–11); C(3–11); M(5–10); Tr(6–9)
Sarcophagula sp.	P(5)
Wohlfahrtia vigil Walk.	M(6, 7)
OTITIDAE:	
Calliopistromyia annulipes Macq.	M(7)
Chaetopsis spp.	P(6, 7, 9); To(6, 9, 10); M(7–9); Tr(6–9)
Chrysomyza aenea (F.)	M(7)
C. demandata (F.)	P(2–12); To(3–11); M(6–10); Tr(5–11)
Delphinia picta (F.)	P(8); To(5–10); M(5–10); Tr(8)
Euxesta nitidiventris Loew.	P(3–11)
E. notata Wied.	P(9); To(4–10); M(5–10); Tr(5–9)
E. spp.	P(4–12); M(6–7)
Notogramma spp.	P(9)
Pseudotephritis spp.	P(4, 5)
Rivellia quadrifasciata Macq.	C(7, 8)
PIOPHILIDAE:	
Piophila casei (L.)	P(3–6, 12); To(5–10); C(5–7, 9); M(5–10); Tr(5)
P. nigriceps (Mg.)	To(9); C(9); Tr(9)
P. pusilla (Mg.)	M(6, 8)
P. spp.	M(5–10); Tr(5, 6)
Prochyliza spp.	C(5, 6, 8–10)
p. xanthostoma Walk.	To(6); C(5, 7–9); M(5, 6)
SEPSIDAE:	
Sepsis spp.	C(3, 6, 7); M(5, 6, 8)
S. punctum L.	P(3)
Themira spp.	C(9); M(6); Tr(5, 8)
T. putris L.	To(6); C(5)
STRATIOMYIDAE:	
Ptecticus sackeni Will.	C(7)
P. testaceus F.	To(5–10); C(3, 6–9); Tr(8)
Hermetia illucens (F.)	P(6)
SYRPHIDAE:	
Copestylum spp.	P(5)
Syritta pipiens (L.)	P(4–6, 10, 11); To(6, 8–10); C(8–10); M(7–9); Tr(8)
Toxomerus spp.	To(9)
Tubifera spp.	To(5, 6, 10)
SYLVICOLIDAE:	
Sylvicola alternatus (Say)	To(5); C(3–12)
S. marginatus (Say)	To(8–10); C(6, 8–11); M(8); Tr(5, 8, 9)

The following families of Diptera were also represented in fly trap collections during the survey:

Phoenix, Mesa-Tempe, Arizona:	Bombyliidae, Borboridae, Culicidae, Drosophilidae, Ephydridae, Helomyzidae, Larvaevoridae, Lonchaeidae, Neriidae, Phyllomyzidae, Therevidae.
Topeka, Lawrence, Kansas:	Asilidae, Bibionidae, Culicidae, Dolichopidae, Drosophilidae, Ephydridae, Helomyzidae, Larvaevoridae, Lauxaniidae, Lonchaeidae.
Charleston, Dunbar, St. Albans, West Virginia:	Culicidae, Dolichopidae, Dorilaidae, Drosophilidae, Ephydridae, Fungivoridae, Helomyzidae, Larvaevoridae, Lauxaniidae, Lonchaeidae, Mycetophilidae, Phoridae, Phyllomyzidae, Rhagionidae, Tetanoceridae, Tipulidae, Tylidae.
Grand Haven, Muskegon, Michigan:	Asilidae, Bibionidae, Culicidae, Chloropidae, Drosophilidae, Helomyzidae, Larvaevoridae, Lonchaeidae, Tetanoceridae, Tipulidae.
Cohoes, Troy, New York:	Borboridae, Culicidae, Dolichopidae, Drosophilidae, Ephydridae, Fungivoridae, Helomyzidae, Larvaevoridae, Lonchaeidae, Phoridae, Tetanoceridae.

*Collection years and areas were: P = Phoenix, Mesa-Tempe, Arizona, 1948 through 1952; To = Topeka, Lawrence, Kansas, 1948 through 1950; C = Charleston, Dunbar, St. Albans, West Virginia, 1948 through 1952; M = Muskegon, Grand Haven, Michigan, 1948 through 1950; Tr = Troy, Cohoes, New York, 1948 through 1950.

** 1= January, 2= February, 3= March, 4= April, 5= May, 6= June, 7= July, 8= August, 9= September, 10= October, 11 =November, 12=December.

***Dash between numbers indicates a period inclusive of both numbers.

At the time of this observation, *C. cadaverina* had been absent from field collections for approximately six weeks. It did not reappear in trap captures until September. Outdoor mean temperatures for the May-September period were May 69.1, June 77.0, July 80.6, August 77.1, September 64.7. Basement temperatures were estimated to be 5 to 10 degrees below exterior readings.

In reviewing the data for the two years of trapping, it will be noted that certain species manifested striking differences in abundance for 1949 and 1950 (*e.g.*, *Calliphora vomitoria* and *Protophormia terrae-novae*, Cohoes, New York). While changes in weather factors often are the basis for such differences, critical analysis of the seasonal prevalence and sampling methods sometimes reduce what seemed to be drastic changes to minimal fluctuations. In the examples cited above, it was found that operational difficulties resulted in a two-week gap in collections in the midsummer of 1950 and that all trap surveys for that year ceased on October 1. By reference to the 1949 data, it was shown that 982 of 1733 *Protophormia terrae-novae* captured were retrieved during the summer weeks not covered in 1950. With *Calliphora vomitoria*, the exclusion of the October collection in 1950 eliminated one of the peak months of prevalence for that species. Situations of this type emphasize the need for careful repetitive surveys over successive years before attempting to correlate fluctuations in prevalence with climatic changes. They also focus attention on the fragmentary and sometimes tenuous nature of so many of the distribution data which are available not only for flies but for other insects as well. In lieu of comprehensive surveys, the accurate plotting of species occurrence within an area even as well populated as the United States appears destined to simulate an evolutionary process.

SUMMARY

The principal minor species of flies trapped at communities in Arizona, New York, Michigan, West Virginia, and Kansas during 1949 and 1950 (*Bufolucilia silvarum*, *Lucilia illustris*, *Cynomyopsis cadaverina*, *Calliphora vomitoria*, *Protophormia terrae-novae*, *Calliphora vicina*, *Fannia canicularis*, *Hydrotaea houghii*, *Euxesta notata*, and *Chrysomyza demandata*) are discussed. Complete species lists, including a monthly chart of occurrence, are presented for 10 municipalities in the five States.

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EGGS OF FLOODWATER MOSQUITOES III (DIPTERA, CULICIDAE). CONDITIONING AND HATCHING OF AEDES VEXANS[1]

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Eggs of floodwater mosquitoes are capable of withstanding adversities such as drought, cold and unfavorable submersion. Once the eggs of a species have been subjected to adversity, a sequence of events called "conditioning" is required to predispose them to respond to the final stimulus. This sequence of events necessary for conditioning varies according to the species. Accordingly some may hatch shortly after the onset of any period of inundation in spring and summer; others respond to a hatching stimulus only as the ice breaks up late in the winter or early in the spring. Eggs of both groups refrain from hatching whenever they are flooded before they have been conditioned or prepared for hatching. Once eggs are conditioned, the ultimate stimulus to hatching of any of the species is a decreasing gradient of oxygen dissolved in the water under which the eggs are submerged (Borg and Horsfall, 1953).

[1]Contribution from the Department of Entomology, University of Illinois.

Funds for the support of this investigation were provided by a grant from the Division of Research Grants, U. S. Public Health Service.

Mr. Robert C. Wallace, Research Assistant, is herewith thanked for aid in obtaining the data contained herein.

Accepted for publication, Feb. 24, 1955.

HATCHING

Aedes vexans represents the group of mosquitoes that hatch shortly after the onset of inundation in the late spring or any time during the summer. Reports in the literature indicate that it is a species that may have one or more generations each year. Likewise records indicate that eggs vary in their response to inundation. Some eggs are capable of hatching within a few days after deposition, or they may survive in favorable sites for a year or more and hatch when the environment is favorable. This discussion is an account of stimuli that condition eggs for hatching as well as of those that cause conditioned eggs to hatch.

More often than not eggs of *Aedes vexans* that have been deposited in natural sites after midsummer are not provided with conditions suitable for hatching. Either the water table remains below them, or they are submerged during the winter when the temperature is unfavorable. All observers agree that eggs hatch during the summer at times when sites where they were deposited are flooded by runoff, rise of water table, or overflow. Observations of conditions surrounding development in the field during the spring of 1952 and that of 1953 showed that eggs hatched only during a short interval immediately after being flooded. Should eggs be submerged by cold (10°C or less) water and remain submerged as the temperature rises, they will not hatch according to observations made in the field. During 1952, one site was continuously submerged from early January to mid-June while another site nearby was dry until it was flooded early in April. All eggs hatched in the latter site during the April flooding, and none hatched in that continuously inundated. Samples taken from debris in the latter site yielded viable eggs that hatched in the laboratory when submerged after a short period of exposure to air at room temperature. Eggs remaining in the site hatched naturally during a mid-summer flooding following a period when the water table had fallen to a level below the surface. These observations together with similar ones made in 1953 show that after a period of proper conditioning, eggs will hatch readily in natural sites. Obviously flooding alone provides an insufficient stimulus to hatching. At the same time submersion is not destructive of the eggs as was shown by the fact that a large series of eggs maintained their viability for 14 days in the laboratory at 25° C. while being submerged in continuously aerated water. When aeration ceased and a hatching stimulus was applied, all eggs hatched.

TABLE I

RELATION BETWEEN KIND OF NONSTERILE HATCHING MEDIUM AND THE RATE OF HATCHING OF CONDITIONED EGGS OF *Aedes vexans* AT A TEMPERATURE OF 25° C IN THE LABORATORY, 1954

MEDIUM		EGGS USED	EGGS HATCHED	
CONTENT	PERCENT	NUMBER	NUMBER	PERCENT
Fresh corn broth	1	29	29	100
Fresh corn broth	1	31	30	97
Fresh corn broth	1	28	27	97
Fresh corn broth	1	29	28	97
Fresh corn broth	1	76	65	86
Fresh corn broth	1	74	59	80
Corn broth (aged 4 hours)	1	26	11	43
Ascorbic acid	0.1	24	20	84
Boiled water	100	76	41	54
Boiled water	100	22	5	23
80°—water	100	82	2	2
60°—water	100	76	1	1
N_2 water	——	72	15	21
N_2 water	——	25	2	8
Aerated tap water	100	10	0	0

Stimuli sufficient to cause hatching of properly conditioned eggs are provided when eggs are submerged in solutions that cause a decrease in the amount of oxygen dissolved in the water. Experiments involving various species have shown that any means for removing oxygen from solution could stimulate hatching, but all means are not equally effective even for conditioned eggs of *Aedes vexans* as is shown in Table I. A broth made by diluting crushed, canned corn was dependably effective only during the time when it was becoming contaminated with microbes. Less than half of the eggs hatched when a grossly contaminated broth was used such as that which had been exposed to laboratory air in an open container for 4 hours prior to its use. A freshly prepared solution of ascorbic acid at a dilution of 1: 1000 was effective. When water that had been boiled and cooled to room temperature in

the absence of air was used as a hatching medium only about half of the eggs responded. Very few eggs hatched in media de-oxygenated by means of bubbled nitrogen. Aerated tap water and that that had been preheated to 80° C and then cooled were ineffective as hatching media.

All of these media except aerated tap water are known to vary in deficiency of dissolved oxygen. Tests with buffered solutions of ascorbic acid showed that the decrease in dissolved oxygen is sudden, and the content of gas remains very low for an interval long enough to permit hatching. Likewise broth while becoming contaminated with microbial growth shows a decline in amount of dissolved oxygen so that within 4 hours or less such media may show a level similar to that in solutions of ascorbic acid. Water that has been boiled and cooled in the absence of oxygen is devoid of oxygen in solution. It is apparent from Table I that those solutions in which the removal of dissolved oxygen was decreased, the hatching stimulus was exerted over a period of 10 or more hours. In dilutions of 1: 1000 some 20 percent of the eggs had hatched within 5 hours, 60 percent of them had hatched within 10 hours, and the rest hatched after 10 hours. Only 9 percent had hatched within 5 hours in dilutions of 1: 2000, and 29 percent had hatched within 10 hours, while over half of the eggs were stimulated 10 or more hours after submersion. As the media were made more dilute, the stimulus was first delayed and ultimately was suppressed. It is apparent from the data in Table II that microbial growth exerted the hatching stimulus sooner in broth having more sustenance than in that of greater dilution. These observations suggest the hypothesis that oxygen in solution was removed more quickly and consequently, the stimulus for hatching was exerted sooner in the more concentrated media, than was the case in those of great dilution.

Since the stimulus for hatching could be in-

TABLE II

Relation between Rate of Dilution of Corn Broth and Rate of Hatching of Eggs of *Aedes vexans* at a Temperature of 25° C in the Laboratory, 1949

Dilution in Water Rate	Eggs Used Number	0–5 Hr.	Percentage of Eggs Hatched		
			5–10 Hr.	10+ Hr.	Total
1: 100	270	81	2	0	83
1: 200	90	78	2	0	80
1: 300	90	75	1	0	76
1: 500	90	79	0	0	79
1: 1000	180	20	40	23	83
1: 2000	180	9	20	40	69
1: 5000	90	0	0	0	0
Aerated water only	60	0	0	0	0

gun after the eggs were submerged yielded the most uniformly high incidence of hatching. The freshly prepared corn broth that required a relatively long period for removal of the oxygen by microbial growth was consistently the best medium. Broth that had supported a growth for 4 hours and from which the greatest part of the oxygen had been removed before eggs were introduced was somewhat less than half as efficient. Boiled water was of the same order of efficiency, as it, too, had had the oxygen removed from solution prior to introduction of the eggs.

Fresh corn broth made with non-sterile, aerated water in all dilutions up to 1: 1000 was equally effective in providing the basic stimulus for hatching conditioned eggs as is shown in Table II. Dilutions of broth at a rate of 1: 2000 were somewhat less effective, and those of 1: 5000 provided no stimulus to hatching. Dilutions up to 1: 500 stimulated practically all eggs to hatch within 5 hours. As dilutions were inhibited and even suppressed by diluting corn broth, an effort was made to see whether a similar effect might be produced by varying the depth of media. Eggs were submerged in shallow dishes in a chamber where no evaporation could take place. Table III shows that less than half of the eggs were stimulated to hatch in broth 3–4 mm. deep. About two-thirds of them were activated in a medium 5 mm. deep. In media over 7 mm. deep, nearly all eggs could be induced to hatch. When the stimulus was exerted in tubes (65 mm. deep), hatching was consistent but slightly less than in broad, shallow dishes.

Embryonic development progresses to completion within 10 days or less in eggs incubated at room temperature of about 25° C as is shown in Table IV. At least two-thirds of the eggs will be able to hatch within 6 days after they are deposited. After 10 days at 25° all may hatch when flooded by a proper medium. When the basic hatching stimulus is applied during the

first 10 days after oviposition any failure to hatch is caused by the lack of maturity of the embryo. After development is complete, irregularities in rates of hatching reflect the state of conditioning of the eggs.

TABLE III

EFFECT OF DEPTH OF CORN BROTH ON THE RATE OF HATCHING OF CONDITIONED EGGS OF *Aedes vexans* AT A TEMPERATURE OF 25° C. IN THE LABORATORY, 1954

DEPTH MM.	EGGS USED NUMBER	EGGS HATCHED	
		NUMBER	PERCENT
3	49	20	41
4	64	22	35
5	40	26	65
7	56	55	98
10	22	20	91
12	54	53	98
65	88	77	92
65	25	22	88
65	74	69	93

TABLE IV

RATE OF DEVELOPMENT OF EGGS OF *Aedes vexans* ON A MOIST SURFACE AT A TEMPERATURE OF 25° IN THE LABORATORY, 1949

AGE OF EGGS	EGGS USED	EGGS HATCHED	
DAYS	NUMBER	NUMBER	PERCENT
6	90	59	65
7	90	70	77
10	90	75	83
11	90	75	83
12	90	70	77
24	90	82	91

TABLE V

EFFECT OF PRE-HATCHING EXPOSURE TO 25° C ON THE CONDITIONING OF EGGS OF *Aedes vexans* THAT HAD BEEN MAINTAINED AT 4° C IN THE LABORATORY, 1954

EXPOSURE DAYS	EGGS USED NUMBER	EGGS HATCHED	
		NUMBER	PERCENT
0	25	0	0
1	29	10	35
2	28	27	96
3	29	28	97

CONDITIONING

Embryonated eggs subject to conditions of drought and cold require periods of conditioning before they may be stimulated to hatch by any media. Some of the adverse variables to which eggs are exposed include drying of the substrate, decrease in atmospheric humidity, exposure to low temperature and premature submersion. These variables were applied in the laboratory to eggs that had been brought from their natural sites. Eggs were removed from the debris, separated from other species and stored in water at temperatures of 4° to 8° C for 3 to 6 months. Groups of eggs were removed from the cold chamber at intervals and were variously treated at room temperature.

Since exposure to cold retards the response of *Aedes vexans* to the basic hatching stimulus, the amount of time required to condition eggs was established. Table V shows that eggs would not hatch when placed directly from the cold chamber into freshly prepared, non-sterile corn broth. About one-third of them could be induced to hatch after they had been kept on a wet surface at room temperature for a day. Two days consistently conditioned all hatchable eggs. Once eggs were conditioned, they remained so for several weeks. In one instance eggs kept at room temperature for 5 months hatched as well as those kept at this temperature for only 2 days.

TABLE VI

EFFECT OF PRE-HATCHING EXPOSURE TO A COMBINATION OF DRY SURFACE AND MOIST AIR ON THE CONDITIONING OF EGGS OF *Aedes vexans* WHILE EXPOSED TO 25–30°C IN THE LABORATORY, 1954

EXPOSURE BEFORE HATCHING DAYS	EGGS USED NUMBER	EGGS HATCHED	
		NUMBER	PERCENT
2	205	194	94
3	24	19	79
3	24	22	92
12	26	26	100
12	21	18	86
0	28	25	90
0	205	193	94

TABLE VII

EFFECT OF PRE-HATCHING EXPOSURE TO A COMBINATION OF DRY AIR AND DRY SURFACE ON THE CONDITIONING OF EGGS OF *Aedes vexans* WHILE EXPOSED TO 24° C IN LABORATORY, 1954

EXPOSURE BEFORE HATCHING HOURS	EGGS USED NUMBER	EGGS HATCHED	
		NUMBER	PERCENT
0	80	73	91
1	26	20	77
4	22	12	54
8	25	12	48
12	24	13	54
24	24	3	12
48	71	3	4
96	79	1	1

Dryness of the atmosphere enveloping eggs affects conditioning far more than dryness of the surface on which eggs are placed as is seen in Tables VI and VII. An exposure of eggs to dry air of the laboratory for only 4 hours

will cause about half of them to fail to respond when the hatching stimulus is applied. When the dryness continues 8 and 12 hours, about half of the eggs still may be stimulated. After 24 hours only one-eighth of the eggs respond, and virtually none will react after 48 and 96 hours of drying in a room. Eggs on dry paper in an atmosphere saturated with moisture, were responsive to hatching stimuli at any time during 12 days (Table VI). Since 1 hour on a dry surface in dry air caused some decrease in response to hatching stimuli and since 12 days (288 hours) showed no depressing effect on the eggs in an atmosphere that was moist, one may see that atmospheric humidity has a marked effect on regulating the preparation of eggs for responding to the final hatching stimulus.

TABLE VIII

THE EFFECT OF PRE-HATCHING SUBMERGENCE IN AERATED WATER ON THE CONDITIONING OF EGGS OF *Aedes vexans* THAT HAD BEEN EXPOSED PREVIOUSLY TO DRY AIR AT 24–30° C IN THE LABORATORY, 1954

PRE-HATCHING TREATMENT		EGGS USED	EGGS HATCHED	
DRY AIR DAYS	AERATED WATER DAYS	NO.	NO.	PERCENT
0	2	138	129	93
−1	2	74	71	96
1	2	24	19	80
2	2	25	16	64
2	1/12	27	9	33
2	1/6	19	9	47
2	1	25	17	68
7	−1	63	16	25
7	1	21	8	38
7	2	22	12	55
14	1	26	3	12
14	2	28	6	21
14	3	28	1	3
14	4	25	2	8
14	5	28	1	3

Eggs that have been exposed to dry air are de-conditioned but may be variably re-conditioned by pre-hatching submersion in aerated water. Thus eggs on a dry surface in an atmosphere of low humidity may not be stimulated to hatch immediately as is shown in Table VII. About four-fifths of these may be induced to respond by submerging them in aerated water for 2 days immediately prior to treating them with a hatching medium (Table VIII). Even two-thirds of those dried for 2 days may be re-conditioned by submersion for 1 day. When eggs have been dried for 7 days, only half of them may be re-conditioned after 2 days of submersion in aerated water. After 14 days of drying virtually no eggs may be induced to hatch.

If the eggs are exposed only to atmosphere of saturated humidity after even a short period of drying, they show no re-conditioning (Tables VI and IX). Drying for no longer than 8 hours at room temperature caused a decline in hatching rate to one-third that expected.

TABLE IX

EFFECT OF PRE-HATCHING EXPOSURE TO ATMOSPHERE OF SATURATED HUMIDITY FOR 2 DAYS ON THE CONDITIONING OF EGGS OF *Aedes vexans* THAT HAD BEEN EXPOSED PREVIOUSLY TO DRY AIR AT 25° C IN THE LABORATORY, 1954

DRY INTERVAL HOURS	EGGS USED NUMBER	EGGS HATCHED	
		NUMBER	PERCENT
0	102	95	93
2	25	20	80
4	25	11	44
8	25	8	32

DISCUSSION

Embryonated eggs of *Aedes vexans* will hatch after (1) proper moistening, (2) aeration, (3) submergence and (4) de-oxygenation. Most eggs in natural sites require conditioning from either a dry, cold, or de-oxygenated state. As a result different regimens may be necessary before hatching will be completed. During the summer eggs are at temperatures suitable for hatching. However, limiting factors such as age of eggs, amount of moisture and amount of dissolved oxygen may be operative. Hatching of eggs in winter is limited by temperature below the threshold. In the spring hatching may be inhibited by adverse concentration of oxygen or lack of water.

Eggs subject to summer weather will hatch after being conditioned in one of three ways. Embryonated ones in moist debris need only the simplest sequence of events, *viz.*, (1) submergence followed by (2) de-oxygenation of the water. Eggs in air-dried debris hatch after a longer series of events such as (1) submergence, (2) de-watering, (3) aeration of moist eggs, (4) submergence and (5) de-oxygenation. Eggs flooded prior to completion of embryonic development require a sequence such as (1) de-watering, (2) aeration of moist eggs, (3) submergence, and (4) de-oxygenation.

Eggs that have passed the winter will hatch after being conditioned in either of two ways after the water temperature has risen above a minimum of about 17° C. Those in moist debris hatch after (1) submergence and (2) de-oxygenation of the water. Others that were submerged at temperatures below the threshold and continued under water afterward hatch after a sequence of events as follows: (1) de-watering, (2) aeration of moist eggs, (3) submergence, and (4) de-oxygenation.

SUMMARY

Embryonated eggs of *Aedes vexans* are able to withstand adversity such as drought, cold and premature submersion often for long periods. Whenever one or a combination of these adversities occurs, eggs must be "conditioned" before they will hatch. From a wet, cold environment eggs are fully conditioned after 48 hours. Eggs on a dry substrate in an atmosphere of saturated humidity require no conditioning. Those in a dry atmosphere rapidly become deconditioned, and those that were dried for only 24 hours could be re-conditioned by soaking them in aerated water for 2 days. After 14 days of drying very few eggs could be induced to hatch.

Eggs of *Aedes vexans* would begin hatching within 6 days after deposition by the female, and within 10 days all that were viable would hatch when submerged in a suitable medium.

The basic hatching stimulus for conditioned eggs may be provided by any medium that will cause a decrease in the content of dissolved oxygen. Media that support microbial growth are excellent hatching media. Aerated water provides no stimulus.

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SOME OBSERVATIONS ON THE NESTING HABITS AND PREY OF CERCERIS CALIFORNICA CRESSON (HYMENOPTERA, SPHECIDAE)[1]

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INTRODUCTION

The predaceous habits of the wasps of the genus *Cerceris* have long been of interest to biologists. The prey of most of the species is limited to the coleopterous family Curculionidae (*s.l.*), a fact which was early discovered in Europe (Latreille, 1809; Bosc, 1813; Westwood, 1836; *et al.*) and confirmed in the New World (Peckham and Peckham, 1898; Abbott, 1928; Rau, 1928; Williams, 1928; Cartwright, 1931; Krombein, 1936, *et seq.*; Fisher, 1944; Strandtmann, 1945; Scullen, 1951). A bruchid-storing species is known from Central America (Rau, 1933), a primarily cerambycid-hunter from the Philippines (Williams, 1919) and chrysomelid-hunters for the Philippines (Williams, *l.c.*) and North America (Strandtmann, 1945). The European *Cerceris rybiensis* Linn., unlike its more orthodox congeners, captures and stores bees of the genus *Halictus* (Walckenaer, 1817; Marchal, 1887), as do certain other European species (Adlerz, 1900, 1903; Ferton, 1901, 1905, *et al.*).

About one hundred and ten years ago the French naturalist, Leon Dufour (1841); published a fascinating account of a species of *Cerceris* which provisioned its nest with buprestid beetles. It was this account, accidentally encountered in his reading, that inspired Jean Henrie Fabre to undertake his classic studies of insect behavior. Although a number of writers have subsequently added to our knowledge of the beetle-catching wasps of the genus *Cerceris*, few have studied these insects with the enthusiasm and penetration of these early French naturalists. Yet their reports, rich in observation,experimentation and speculation are scarcely referred to in recent literature, and questions clearly answered, by Fabre in particular, have been raised by recent authors, apparently unaware of his painstaking labors.

Not the least of the remarkable facts discovered and analyzed by the early naturalists was the discrimination of the different species of *Cerceris* in the selection of their prey, some selecting only weevils, others buprestids. Dufour, commenting upon the fact that of 450 beetles removed from the cells of *Cerceris bupresticidis* all were buprestids, but representing very diverse and unlike types (*i.e.*, the modern genera *Buprestis, Chrysobothris, Melanophila, Agrilus*, etc.), remarked, "Quel prix Latreille n'autrail-il pas attaché au suffrage de ce Cerceris en faveur de la methóde naturelle." This discrimination was not only evident in a single locality, but persisted in different areas with different vegetation, although of necessity the species composition of the prey changed. Fabre offered *Buprestis* to females of *Cerceris tuberculata*, a weevil-storing species, and they always refused them although they would readily accept various kinds of curculionids which represented species they had never seen before.

Another significant fact discovered by Dufour was that the beetles stored by *Cerceris* did not

[1]Accepted for publication, March 17, 1955.

dry up or deteriorate as did freshly killed beetles. He concluded that the wasps injected a preserving fluid by means of the sting. Fabre was not satisfied with this explanation and he undertook a series of ingenious experiments which demonstrated that the beetles were paralyzed. Through careful observation he determined that the sting was inserted medially between the pro- and mesosternum. By injecting ammonia into the same spot with a pen nib, he was able to produce the same effect as the wasp obtained by stinging. However, this was only true of weevils, buprestids, and scarabs, which have the thoracic ganglia approximate or fused; not of carabids and certain cerambycids, tenebrionids and other beetles in which the ganglia are far apart. From these experiments Fabre concluded that probably only a few families of beetles were suitable for *Cerceris* to collect and store.

Clausen (1940) comments that "Fabre (1879), in his study of *Cerceris tuberculata* Vill., found that the weevils stored in the nest were, with very few exceptions, of a single species, *Cleonus ophthalmicus* Rossi. This limitation is apparently correlated with size; for the *Cerceris* is the largest species known in the section where it was studied, and the weevil species is likewise the largest of the family available. The beetles are nearly twice as large by weight as the wasps that prey upon them. In contrast to this limitation in hosts, the prey of *C. arenaria* L. and *C. ferreri* Lind. comprise a number of genera."

The present study was undertaken in order to learn something of the life history of a buprestid-storing species, *Cerceris californica* Cresson (Table I). However, when buprestids were taken from female wasps, in order to determine which species were being stored, it was found that individual females varied considerably in their selection of prey. These differences in prey-collecting habits of individual wasps were even more clearly evident when the contents of the cells of each burrow had been mounted and segregated with the female concerned. For this reason, the following account is presented in two parts. First is a discussion of the activities of *C. californica* around the nesting site, including such information on burrow construction and other habits of the wasp and its parasites as could be determined by the excavation of the site. Secondly, the 25 female wasps and the approximately 700 buprestids stored by them are analysed in an attempt to determine why the provisions of some individuals should differ so strikingly from others.

LOCALITY AND NESTING SITE

The observations here reported were made in the San Dimas Experimental Forest of the California Forest and Range Experiment Station, United States Forest Service. This experimental area covers 17,000 acres in the San Gabriel Mountains of southern California and is used as a watershed-research laboratory. Our study was conducted near the main headquarters at Tanbark Flat, where *Cerceris californica* Cresson was nesting.

The nesting site was discovered in late June, 1952, and the first extensive observations on the activities of the wasp were made on June 30th. On this day 13 burrows were located, mapped, and activity in the area recorded from 7 a.m. until 1:30 p.m., from 3 to 3:30 p.m., and again at 5 and 6 p.m. No observations were made on July 1st, but on July 2nd activity was followed from 7 a.m. until 1 p.m. and again at 3:15 and 3:30 p.m. On July 3rd activity was recorded from 7 a.m. until 11:30 a.m. for 17 burrows. Throughout this period the weather remained clear and warm with almost no wind. On the morning of July 4th females were collected as they returned with their first prey to these and 8 additional burrows. Following each capture, the burrows were filled with liquid Plaster of Paris, and later all of the burrows and their associated cells were excavated. The present account is based primarily on these data although supplementary information on the habits of various species of buprestid prey were gathered between June 22 and July 28th, 1952 and during a similar period in 1950.

The wasps had concentrated their nests near one corner of a one story building on the south side of a parking area. At this location a small strip of nearly bare soil about eighteen inches wide contained the majority of the active burrows. This strip was bounded on the southeast side by the edge of the building and on the northeast end and northwest side by asphalt paving. The building had a roof which slanted down to the northwest with a twelve inch overhang. Since there were no gutters on the roof, during periods of precipitation a considerable amount of rainwater was concentrated in the area where the wasps were nesting. In addition, runoff from the asphalt parking area also concentrated some rainwater on the site, although the soil surface had not been eroded by water action. The soil was a fine grained, hard packed sand derived from decomposed sandstone. When our excavations were made on July 4th, the top inch of soil was dry but at a depth of three or four inches the soil was moist enough to be packed. The few grasses and vascular plants that were growing on the site did not interfere with nesting by *Cerceris* since their root systems did not penetrate more than a few inches below the surface. However, the proximity of the burrows to the building produced a significant pattern of sunlight and shade over the burrow entrances during the course of each day (fig. 1).

In the early morning, prior to 7:30 a.m., all of the burrows were in sunlight which passed by the east corner of the adjacent building. As

the sun rose, the shadow of the building moved progressively from west to east and by approximately 11 a.m. the entire nesting site was in shade. It remained in the shade until the sunlight passed over the top of the building and reached the northwest edge of the nesting site at 12:30 p.m. This pattern of alternating sunlight and shade definitely influenced the activity of the females in the five burrows located at the southwest end of the area, and of these, the four farthest to the

TABLE I

SOME NORTH AMERICAN BUPRESTID-STORING CERCERIS

Cerceris spp.	PREY	LOCALITY	AUTHORITY
argyrotricha Rohwer	*Acmaeodera pulchella* (Hbst.)	Texas	Scullen, 1951
californica Cresson	*Acmaeodera acuta* LeConte	Calif.	new record
	Acmaeodera adenostomae Cazier	Calif.	new record
	Acmaeodera angelica Fall	Calif.	new record
	Acmaeodera coquilletti Fall	Calif.	new record
	Acmaeodera dohrni Horn	Calif.	new record
	Acmaeodera dolorosa Fall	Calif.	new record
	Acmaeodera fenyesi Fall	Calif.	new record
	Acmaeodera gemina Horn	Calif.	new record
	Acmaeodera hepburni LeConte	Calif.	new record
	Acmaeodera holsteni White	Calif.	new record
	Acmaeodera jocosa Fall	Calif.	new record
	Acmaeodera nexa Fall	Calif.	new record
	Acmaeodera perlanosa Timberlake	Calif.	new record
	Acmaeodera plagiaticauda Horn	Calif.	new record
	Acmaeodera prorsa Fall	Calif.	new record
	Acmaeodera quadriseriata Fall	Calif.	new record
	Acmaeodera sinuata Van Dyke	Calif.	new record
	Agrilus angelicus Horn	Calif.	new record
	Agrilus blandus Horn	Calif.	new record
	Agrilus politus (Say)	Calif.	new record
	Anthaxia aeneogaster Cast.	Calif.	new record
	Chrysobothris deleta LeConte	Calif.	new record
	Chrysobothris lucana Horn	Calif.	new record
	Chrysobothris femorata (Olivier)	Calif.	new record
fumipennis Say	*Actenodes acornis* (Say)	S. C.	Cartwright, 1931
	Agrilus arcuatus (Say)	S. C.	Cartwright, 1931
	Agrilus bilineatus (Web.)	S. C.	Cartwright, 1931
	Agrilus objectus Horn	Mo.	Rau & Rau, 1918
	Buprestis consularis Gory	S. C.	Cartwright, 1931
	Buprestis fasciata (Fabr.)	S. C.	Cartwright, 1931
	Buprestis lineata (Fabr.)	N. Y.	Grossbeck, 1912
		S. C.	Cartwright, 1931
	Buprestis maculipennis Gory	S. C.	Cartwright, 1931
	Buprestis rufipes (Oliv.)	S. C.	Cartwright, 1931
	Buprestis striata (Fabr.)	S. C.	Cartwright, 1931
	Chrysobothris blanchardi Horn	S. C.	Cartwright, 1931
	Chrysobothris dentipes (Germ.)	—	Ashmead, 1896
		S. C.	Cartwright, 1931
	Chrysobothris femorata (Oliv.)	Wisc.	Peckham & Peckham, 1898
		S. C.	Cartwright, 1931
	Chrysobothris floricola Gory	N. Y.	Grossbeck, 1912
		S. C.	Cartwright, 1931
	Chrysobothris lesueuri Cast.	S. C.	Cartwright, 1931
	Chrysobothris sexsignata (Say)	S. C.	Cartwright, 1931
	Chrysobothris verdigripennis Frost	S. C.	Cartwright, 1931
	Dicerca divaricata (Say)	—	Scullen, 1951
	Dicerca lurida (Fabr.)	S. C.	Cartwright, 1931
	Dicerca obscura (Fabr.)	S. C.	Cartwright, 1931
	Dicerca punctulata (Schön.)	N. Y.	Grossbeck, 1912
	Dicerca spreta (Gory)	S. C.	Cartwright, 1931
	Dicerca tuberculata (Cast.)	S. C.	Cartwright, 1931
species?	*Nanularia cupreofusca* Casey	Calif.	VanDyke, 1942

southwest were most critically affected. The females in burrows which were in sunlight until 9:30 a.m. made their first flight (based on twenty-four records) between 9:00 and 10:49 a.m. with most of the individuals leaving their burrows within a few minutes of 10 a.m. The female, whose burrow was fifth from the southwest end, was not seen until July 2nd and did not leave her burrow until 11:04 a.m. on July 3rd. The females in the other four burrows were recorded as leaving their burrows for their first trip on five occasions at 10:58 a.m., 11:51 a.m., 12 N., 12:45 p.m., and 1:05 p.m., and records of "no activity" were also made on five occasions.

BURROW LOCATION AND STRUCTURE

Most of the burrow entrances were located along the margin of the asphalt pavement (fig. 1), although a few were several inches from the pavement and others were scattered in the bare area to the southwest. Each entrance was surrounded by a conspicuous tumulus of excavated earth which measured three or more inches in diameter. The entrance was usually in the center of the tumulus except where the burrow was directly against the raised asphalt pavement. In these cases the soil was accumulated away from the pavement.

The burrow of *C. californica* (fig. 2) is circular in cross section with a slightly smaller diameter near the surface. The shaft is vertical for several centimeters, then curves gradually for several additional centimeters. Although the burrow continues to curve, a plug of moist sand several centimeters in length prevents the obtaining of a complete plaster cast of the burrow. The curving portion is open beneath the plug and leads to a horizontal cell at a depth of less than twenty centimeters. The physical proportions of each of the 27 burrows varied with the size of the female which had constructed it and these variations were considerable since the smallest female was less than four-fifths the size of the largest. The dimensions of part of a burrow constructed by one of the smallest females were as follows: diameter near surface about 5 mm., greatest diameter about 6 mm., depth of burrow to plug 55 mm. The dimensions of part of a burrow constructed by one of the largest females were as follows: diameter near surface more than 6 mm., greatest diameter 7.5 mm., depth of burrow to plug 90 mm. The length of the plug varied only slightly and averaged 55 mm. in length. No correlation could be found between the size of the female and the depth of the cells. However, there was a direct correlation between the depth of the cells and what was presumed to be a gradually retreating moisture level in the nesting site since there was no rain in the area during the summer months.

The cell being currently provisioned is always found at the end of the curved burrow, and is horizontal. It is rounded at its base, the walls are only slightly curved, the sides are subparallel, and the entrance is narrowed. Cells varied in length from 12 to 17 mm. and in greatest width from 8 to 9.5 mm.; diameter at the entrance was from 6 to 8 mm. The cell walls are finely smoothed. Each completed cell is sealed with a tight plug of sand about 1 cm. deep. The burrow is then excavated deeper to provide for the next cell.

DAILY ACTIVITY

The following generalized account of the daily activity pattern of *Cerceris californica* does not apply in detail to the females with the five most westerly burrows (fig. 1), since their behavior was obviously affected by prolonged shading of this portion of the nesting site.

The first evidence of wasp activity in the morning usually involved movement of the entrance plugs. These movements were of several types. Usually, the plugs were moved slightly and later pulled down into the burrow, after which the head of the wasp would appear at the entrance. Sometimes they were first pushed upward and portions would break off and add to the tumulus. In one instance, a female was observed to push the plug completely out on to the surface without withdrawing any part of it. The movements of the plug were difficult to see and were only recorded eight times. On July 2nd, plugs of three burrows were first seen to move at 7:47, 7:59, and 8:16 a.m., and these same burrows were opened at 8:16, 8:09, and 9:41, respectively. On July 3rd, similar activity for four burrows was recorded at 7:42, 7:47, 7:57, and 8:07 a.m. and they were opened at 9:01, 8:30, 8:37, and 8:30, respectively. On this same date two other burrows were opened at 7:28 and 7:37 a.m., without plug movements having been noticed.

The time of first opening of the burrows varied from as early as 7:28 a.m. to as late as 9:41 a.m., but in most cases this occurred between 8 and 9 a.m. On one occasion three females opened their burrows in the usual manner but, without leaving, replugged them more than an hour later and reopened them shortly afterwards. As indicated above, after opening the burrow, the head of the female may be seen just within the entrance. Later, she moves to the lip of the burrow and after a few seconds takes off in flight. The time between the first opening of the burrow and the first flight varied from 38 to 120 minutes, in most cases involving an hour or more.

In general, the burrows were closed for the day between 11:30 a.m. and 3:30 p.m., and remained closed until the following morning. The closing plugs were of moist sand and usually protruded slightly from the surrounding tumulus. However, in some cases the plug was below the level of the tumulus; in a few instances, several

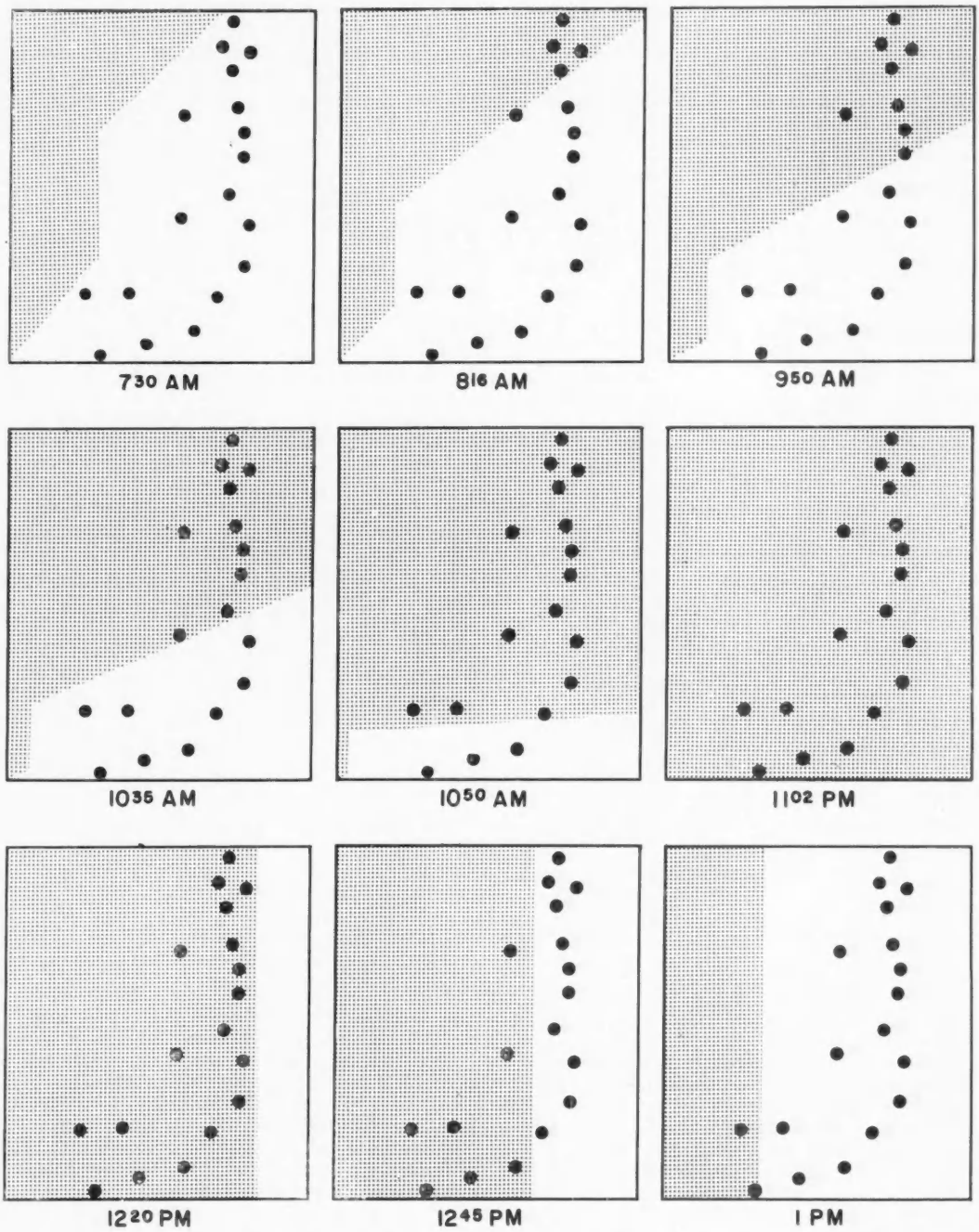

FIG. 1. Patterns of sunlight and shade over burrow entrances on June 30, 1952.

centimeters below the surface. Sometimes it was difficult to determine whether the latter situation obtained or whether the burrows were unplugged. Furthermore, this variation in plugging was associated with individual burrows.

When leaving the burrow for the first time on a given day, most females fly a characteristic "reconnoitering" pattern. This involves circling the entrance several times at a distance of a few inches, then at an increased elevation and distance, followed by a few rapid and irregular flights over the nesting site. The flight away from the site was nearly always in a straight line, with the wasps slowly rising higher in the air as they progressed. In most cases, the wasps flew down the roadway to the east, only rarely northward over the paved area to the hillside beyond. The time of the first flight varied from 9:10 to 11:04 a.m., and not infrequently the wasp returned from her first trip without prey. Twenty-nine first flights were recorded as follows: 9:00 to 9:30 a.m., 2 flights (1 without prey); 9:31 to 9:45, 5 flights (2 without prey); 9:46 to 10:00, 7 flights (2 without prey); 10:01 to 10:30, 11 flights (2 without prey); 10:31 to 11:00, 3 flights (1 without prey); and 1 flight at 11:04 a.m. from which the female returned with a buprestid.

FIG. 2. Burrow diagram of *Cerceris californica* Cresson.

The time required to leave the nesting site, capture a buprestid and return to the burrow was recorded for 65 flights. These varied from 30 seconds to 39 minutes. However, almost three-quarters of the trips were of 15 minutes duration or less: 18 trips or 27.7 percent were not over five minutes; 20 trips or 30.8 percent were between 6 and 10 minutes; 10 trips or 15.4 percent, 11 to 15 minutes; 8 trips or 12.3 percent, 16 to 20 minutes; 5 trips or 7.7 percent were 21 to 25 minutes; 4 trips or 6.2 percent were from 26 to 39 minutes. Because of the wide variation in the length of time for each trip, these periods were analyzed for possible correlations with time of day, size of wasp, the number of earlier trips made on the same day, and finally, the age of the wasp as indicated by number of completed cells.

The possible effect of time of day was examined for the fifty-nine trips recorded between 9:30 a.m. and 12 noon with the following results; 9 trips between 9:30 and 10:00 a.m. averaged 10 minutes with 44 percent being 10 minutes or less; 17 trips between 10:01 and 10:30 averaged 12 minutes with 53 percent 10 minutes or less; 13 trips between 10:31 and 11:00 averaged 9 minutes with 77 percent 10 minutes or less; 13 between 11:01 and 11:30 averaged 14 minutes with 44 percent 10 minutes or less; and 7 trips between 11:31 and 12 noon averaged 7 minutes with 86 percent 10 minutes or less. A further test of the effect of time of day was made by summing up all of the trips which were shorter or longer than the previous trip. Nine trips were shorter, two of equal duration and seven were longer than the previous trip. These data do not show any correlation between time of day and length of trips. Although the reasons for this are not clear, it seems likely that greater activity on the part of the wasps as the temperature rises might be offset by the greater activity of their prey. Apparently the females of this species of *Cerceris* do not regularly visit flowers for nectar, and in the two years that this area was heavily collected by about 70 entomologists, no females were taken on flowers. Thus the time spent away from the burrow presumably reflected search for prey.

Neither the size of the individual wasps nor the number of previous trips made on a given day showed any correlation with the length of time required for a trip. However, the number of cells previously provisioned (an index of the previous experience of the individual) showed a clear correlation with the length of the trips. For example, two females which were provisioning their first cell were timed on five occasions at 20, 21, 22, 26, and 39 minutes per trip. Two other females which had provisioned three cells, were timed on twelve occasions at 4, 7, 9, 10, 11, 11, 12, 12, 13, 14, 22 and 22 minutes per trip. Finally, two females, one with 8 and the other with 7 cells completed, were timed on eleven

occasions at ½, 4, 5, 5, 6, 6, 7, 7, 8, 8 and 10 minutes per trip. It is interesting to note that Krombein (1953b) also observed considerable variation in the time required for individual females of *Cerceris robertsonii* Fox to capture and return to their burrow with a chrysomelid beetle *Rhabdopterus picipes* (Olivier) and further that one of the most efficient providers was later found to have provisioned nine cells.

Prey was taken from a number of the wasps on June 30th and July 2nd. The females responded by immediately flying off to return with another buprestid, even when as many as five beetles were taken from a single female on successive trips. Nine such flights were timed at 1, 5, 5, 6, 6, 10, 10, 14, and 20 minutes.

When returning to the burrow with prey, the female alights at the entrance and enters immediately with the buprestid pressed tightly to the underside of her body, upside down and head forward. This behavior was modified when one of the parasitic flies approached the wasp before she reached the burrow (see below). In one case, a wasp was apparently carrying the prey right side up and turned it over just before entering the burrow. Usually within a minute after entering with prey, the burrow is plugged from below.

The time a female remained in the burrow after entering with prey varied from 5 minutes to 63 minutes. However, more than fifty percent of the 46 periods recorded fell within a range of 9 to 17 minutes, and within this range the greatest frequencies were 9 to 11 minutes. A positive correlation existed between the time spent in the burrow between trips for prey and the number of trips the wasp had made previously. Two individuals provisioning their first cell were timed on five occasions and four of these periods were the longest recorded: 20, 34, 46, 60, and 63 minutes. Two individuals provisioning their third and fourth cells were both recorded for the shortest and also for the next longest periods between trips: the one with four cells at 5, 8, 8, 10, 11, 14, 16, 18, and 32 minutes, the other, 5 and 33 minutes. Three additional females, which had provisioned 7, 6 and 5 cells respectively, were recorded between trips as follows: 9, 11, 11, 11, 17 and 24 minutes; 9, 9, 9, 10, 10, 14 and 21 minutes; and 13, 17, 17, and 25 minutes. Although these data are scant, they indicate that females which are provisioning their first cell take considerably longer to perform what are assumed to be the same functions between trips as do females which have been provisioning for a longer period of time.

Some of the activities of the wasps within the burrows after returning with prey can be inferred from the situations found when all of the burrows were excavated. As stated previously, each female was captured with her prey as she returned to her burrow on the morning of July 4th. As a result, the characteristics of the plug which she brings to the surface after entering with her prey was not determined. Each burrow was found to have a lower plugged portion which varied in depth but only slightly in length (averaging about 55 mm.). Many of these plugs contained from one to eleven buprestids which were packed at random in the upper portion of the plug. The beetles were facing downward, and a few became active after removal from the plug. Apparently, as the wasp returns to her burrow, she immediately plugs the entrance and then manipulates the new prey down into the lower plug. It seems likely, considering the relatively long period that the wasp remains in the burrow with the new prey, that some of this time may be spent on other activities. One possibility is that the female might re-manipulate the buprestids which had been previously stored in the plug. A re-examination of some of the time periods involved suggests such a possibility. For example, an individual recorded as having three cells spent 9, 15 and 7 minutes in the burrow on July 2nd at which time she presumably had at least 3, 4 and 5 buprestids in the plug. On July 3rd these periods were 20, 22, and 21 minutes when she presumably had at least 6, 7 and 8 buprestids in the plug. The female with four cells and nine recorded periods reported above was observed bringing in 6 buprestids on July 2nd, 5 buprestids on July 3rd. When her burrow was excavated, a newly provisioned cell contained an egg and 11 buprestids (none were in the plug). On July 2nd this female was in the burrow for 32 minutes after returning with the first buprestid and then for periods of 10, 8, 8 and 5 minutes with 2, 3, 4, and 5 buprestids. On July 3rd the periods were 16, 18, 14 and 10 minutes with 7, 8, 9, and 10 buprestids. Finally, the females with seven and six cells completed had 8 or 9 buprestids in their plugs and spent similar periods in their burrows between trips for prey, while the female which had provisioned five cells spent longer periods in the burrow and was later found to have 12 buprestids embedded in the plug.

The habit of paralyzing the insects stored for larval food is well known for many groups of wasps and was investigated by Fabre (1879) for *Cerceris tuberculata* Vill. He found this species bringing in already paralyzed weevils, and when he was able to substitute normal weevils for those being brought in by the wasps, they would immediately sting the substituted weevils before taking them into their burrows. No positive evidence on the stinging of the buprestids was obtained. All buprestids taken from females as they returned to the nesting site were extremely active and capable of flight and remained active in pill boxes for considerable periods of time after removal from the wasp. A number of those from the deep plugs where they had been stored

the previous day were also active when removed. However, no active buprestids were found in any of the numerous cells excavated. This situation is apparently comparable to that reported for *Eucerceris ruficeps* Scullen (Linsley and MacSwain, 1954) where it was postulated that the wasps either do not paralyze the prey until they are ready to place them in the cells or that the toxin has a delayed effect upon the nervous system.

The cells are constructed and provisioned between the final closure of the burrow, in the late morning or early afternoon, and the morning of the next day. On July 4th the burrows of nine wasps that had been recorded bringing in prey on both July 2nd and 3rd were excavated. Two of these had 11 and 12 buprestids in their plugs and were captured while bringing in additional prey. Another had apparently provisioned a cell between July 2nd and 3rd and had only 6 buprestids in the plug. The other six females, each of which was captured bringing in prey on July 4th, had no buprestids in their plugs and also had a freshly provisioned cell containing an egg. In no cases were freshly constructed but unprovisioned cells found. It seems likely that cells are constructed and provisioned in one afternoon following several days of accumulating prey in the plug.

The amount of time required to capture sufficient prey to provision a single cell apparently varies considerably. When females were foraging, they captured from one to seven buprestids in a single day. Those active on both July 2nd and 3rd provide the clearest picture of the ability of the wasp to locate and capture prey. One female provisioning for her first cell captured two buprestids on July 2nd and two on July 3rd. On July 4th she was found to have placed all four in a cell, oviposited, and sealed the cell. Another female successively captured six and five buprestids and placed all eleven in a single cell. More commonly females had captured four to eight buprestids on July 2nd and 3rd and provisioned cells with more beetles than had been captured on these two days. Finally, two females which had 11 and 12 buprestids in their plugs on July 4th had not previously provisioned any cells with as many prey as this. From these data it is evident that while sufficient prey to provision a cell may be accumulated in two days, a greater time period is usually involved.

The number of buprestids placed in any one cell is extremely variable and apparently controlled by a number of factors. In the first place, the distribution by numbers of buprestids in 145 cells gave a bimodal curve which on the basis of a limited number of rearing records appears to be correlated with the sex of the progeny. One mode at 5 and 6 buprestids per cell correlates with male progeny, the other at 10 and 11 with female progeny. Secondly, there seems to be evidence that the number of beetles placed in a cell partially reflects the relative success of the wasp in capturing prey. Thirdly, the number of prey depends in part on the size of the prey species which, as shown below, is largely dependent on the size of the individual female wasp. Of the four cells containing the greatest number of prey, three had twelve *Acmaeodera* each as follows: one, 12 *adenostomae*, another, 6 *adenostomae* and 6 *nexa*, the third, 8 *adenostomae*, 3 *nexa*, and 1 *holsteni*. The fourth cell had eighteen *Acmaeodera:* 14 *adenostomae*, 2 *nexa*, and 2 *jocosa*. *Acmaeodera adenostomae* and *A. nexa* were the two smallest of the most abundant species in the area.

Prior to placing the buprestids in the cells they are thoroughly cleaned. When first captured many of the beetles are covered with pollen grains and other detritus, much of which is lost when they are stored in the sand plug in the burrow. However, a considerable amount of this material remains within minor declivities of the exoskeleton and most of it is finally removed before the buprestids are placed into the cells.

Within each cell (fig. 2) the prey are usually placed on their backs and invariably oriented with their heads toward the base of the cell. Most of these specimens have the wings folded under the elytra although a few have them partially unfolded. Commonly, one or more of the beetles in each cell were found to have the head strongly twisted so that one side was abnormally inserted into the prothorax the other exserted so that a portion of the cervical membrane was exposed. Whether this distortion results from stinging by the female wasp or from some special manipulation of the prey is not clear. In any event, the elongate cylindrical egg is firmly attached to the median venter of the uppermost buprestid with the anterior end near the posterior margin of the head.

Upon hatching, the young larva commences feeding in the area of the mouthparts of the buprestid upon which the egg was laid. Subsequently the head and thorax of the prey are hollowed out and finally the abdomen. In most cases only the heads of the buprestids are detached during feeding, more rarely the thorax also. Detailed information on the length of the stages was not obtained although that of the egg would appear to be a week or less. Upon completion of feeding on the stored buprestids the full grown larva ties the fragments together with a loose network of silk then fashions the tightly woven cocoon, so characteristic of the family, within this framework. The larva then overwinters in the cocoon and transforms the following summer.

In studies of aculeate Hymenoptera evidence is frequently accumulated that appears to indicate that the species is double-brooded. In most cases, when there are opportunities to make detailed studies of the life cycle, it is found that the species has a single generation a year. In

the authors' experience the confusion has most commonly been due to a protracted period of adult emergence in a restricted habitat. Studies of a very small population of *Eucerceris ruficeps* (Linsley and MacSwain, 1954) led the authors to state that "although this species is known at Antioch from about a dozen females collected in August and September, the burrow evidence might be interpreted to indicate that the species is double-brooded". The same type of evidence was found in some of the burrows of *Cerceris californica*, namely some cells with eggs and young larvae, others with cocoons from which adults shortly emerged. It now seems clear that the situation is one of protracted emergence in which females re-use old burrows of the previous season when they are available. This conclusion resulted from the discovery of burrows in which the associated cells contained only eggs or cocoons. Of the 74 cells for which the probable instar of the wasp was recorded 21 contained eggs, 18 very young larvae, 6 medium sized to almost mature feeding larvae and 29 mature larvae in cocoons. However, this apparently disproportionate distribution of the developmental stages cannot be considered as conclusive proof of a single generation since Krombein (1953b) has reported that the time from hatching of egg to cocoon formation may be as short as six days for *Cerceris robertsonii*.

PARASITES

Several parasitic insects associated with *Cerceris californica* were encountered around the burrow entrances or in old and new cells.

Four unemerged females and one male of a mutillid wasp, *Dasymutilla coccineohirta* (Blake)[2], were taken from cells of the previous year and several other females were active in the nesting site in the morning and evening during the period of this study. Since little has been recorded about the habits of this species around the burrows of a known host the activity of a female on the morning of July 2nd is here reported. This female was first seen in the area at 8:24 a.m., at which time all but two of the cercerid burrows were closed. She was digging into what appeared to be a completed burrow between two active burrows near the edge of the pavement at the side of the nesting site. The digging soon ceased, however, and the mutillid wandered irregularly over the entire nesting site examining mounds or occupied burrows for a period of about ten minutes. During this time, she made no attempt to funnel into any of the numerous burrows which she examined although she placed her head in the entrance of one of the burrows which had been opened earlier by its inhabitant. The wasp in this burrow immediately came partially out of the entrance and the mutillid moved away. At the end of this ten minute examining period the female returned to the burrow where she had first been seen and started digging at 8:38 a.m. She excavated rapidly, pushing the earth behind her and by 8:43 was out of sight. A minute later considerable squeaking and buzzing was heard and the mutillid dug herself out and ran away from the burrow for a distance of more than 12 inches, then slowed her pace and recommenced examination of the general area. The burrow into which she had tunneled was later found to contain a female cercerid. The mutillid was not seen again after 8:50 a.m.

Other observations on the habits of species of *Dasymutilla* have led us to believe that these wasps normally parasitize completed cells of their hosts and for this reason are usually active in the latter part of the host season and for some time after the host nesting activity has ceased.

Species of sarcophagid [3] flies were also observed around the nesting site and a few general notes on their habits were made. However, the task of observing and tabulating the activities of the cercerid wasps prevented other than minor observations of the flies.

The most abundant species in the nesting area was the small species *Metopia leucocephala* (Rossi) and a number of adults of this species were later reared from larvae found in the cells or pupae from near the cells. The first activity by this species on July 2nd was recorded at 8:41 a.m. when a female was observed to enter just inside the opening of a burrow and to leave immediately when the female wasp appeared in the entrance. On July 3rd the first fly was seen to visit another open burrow at 8:13 a.m. On a number of other occasions, prior to the wasps leaving the burrows for their first trip, this same behavior was recorded, although in four cases the flies remained in the burrows for periods of 2 to 4 seconds. However, the major portion of the flies activity consisted of staying on the surface of the ground, commonly facing one of the wasp burrows. On the emergence of a wasp on both the first and on subsequent trips two patterns of activity were recorded although their possible significance was not studied. As a wasp flew away from the nesting site a fly would commonly follow it for several feet and then return. On other and more numerous occasions a fly in the immediate vicinity of a burrow from which a female had just left would enter this burrow immediately and remain out of sight for from 6 to 10 seconds.

When *C. californica* females returned with prey, females of *M. leucocephala* would occasionally fly out and meet them before they reached the nesting site or more commonly just as they reached the site. In such cases the fly would orient itself an inch or more behind the flying wasp and maintain this position even when the

[2]Identified by P. D. Hurd.

[3]Identifications by M. T. James.

wasps flight pattern was very irregular. The flight of the flies was so synchronized with that of the cercerid that when the wasp made a sudden change in the direction the fly made the same change so quickly that no time lag could be observed. When a wasp carrying prey was being followed by a fly she spent a longer period of time flying around the nesting site than when not accompanied by a fly, and would occasionally leave the area briefly and return with the fly still accompanying her. The flies did not contact the wasp or prey even while the wasp was entering her burrow. After the cercerid entered the burrow the fly would rest on the ground an inch or more from the entrance and facing the entrance. The fly would remain in this position for ten to fifteen minutes and under these circumstances it could be examined with a hand lens without disturbing it. If the wasp remained in the burrow for a longer period of time the fly would soon begin to make short flights around and away from the burrow and eventually leave if the wasp did not leave shortly. In most cases the wasp would unplug her burrow and fly away within ten minutes, in which case, as previously mentioned, the fly would enter the open burrow and remain inside for from 6 to 10 seconds.

The activity of a *Metopia* female within a burrow was not determined although it seems likely that she larviposits several times in the lower plug in which the wasps deposit their prey before placing them in the cells. It would appear to be physically impossible for the fly to penetrate the long earthern plug of the wasp and approach the cells which are provisioned at a lower level. In a number of cells, sarcophagid larvae were found feeding on the stored buprestids and in one cell a larva was feeding on the egg of the wasp.[4] Only the larval stage of the fly was found in the cells but several of these were reared to the adult. Additional adults were reared from pupae taken from the earth near the burrows and in one case from the plug of one burrow.

Two other species of sarcophagids, *Amobia floridensis* (Townsend) and *Senotainia trilineata* (Van der Wulp), were active around the burrows of *C. californica* but in small numbers.

No exact data on the percentage of parasitism or incidence of mold was recorded although the combined losses would be in excess of twenty percent of the cells provisioned.

FACTORS INFLUENCING SELECTION OF PREY

(a) Habitat relationships of buprestid prey.

The vegetation associations available to *Cerceris californica* at Tanbark Flat as sources of prey have been listed by Wright and Horton (1951) in connection with their study of the vertebrate fauna. The more important of these are as follows:

Chamise-chaparral Association. Open to fairly dense stands of *Adenostoma fasciculatum* H. & A., *Ceanothus crassifolius* Torrey and *Arctostaphylos glauca* Lindl. Three common species of *Acmaeodera* (*jocosa*, *holsteni*, *adenostomae*) were associated with *Adenostoma*. It was the dominant plant in this Association and a favorite source for prey. In 1951, 76 percent of the buprestids stored were from this source; in 1952, 60 percent (Table II). *Ceanothus* was also a good host, yielding *Acmaeodera sinuata*, *A. dohrni*, *A. prorsa*, *A. dolorosa*, *A. angelica*, *A. nexa*, *Chrysobothris deleta* and *C. lucana*. In 1951, 18 percent of the buprestids stored were from this plant; in 1952, 30 percent. *Arctostaphylos* was a poor buprestid host, yielding but one rare species, *Acmaeodera plagiaticauda*. Two wasps each stored one of these in 1952, none in 1951.

Oak-chaparral Association. Composed of dense stands of *Quercus dumosa* Nutt. and *Q. wislizenii* A.DC. Associated buprestids included *Acmaeodera coquilletti*, *A. hepburni*, *A. acuta*, *Agrilus angelicus* and *Anthaxia aeneogaster*. Two percent of the 1951 prey and six percent of the 1952 prey appeared to be from this source,perhaps from areas of interdigitation or overlap with chamise chaparral.

Stream-woodland Association. Dominant species included *Quercus agrifolia* Nee, *Platanus racemosa* Nutt., *Acer macrophyllum* Pursh., *Populus trichocarpa* T. & G., *Alnus rhombifolia* Nutt., and *Salix* species. Although this association supported a buprestid fauna, especially *Populus* and *Salix*, it was not utilized as a source for prey in so far as could be determined. However, in another locality 6 miles northwest of Tracy, San Joaquin County, *Cerceris californica* appeared to be working this habitat exclusively.

Within easy flight range of the nesting site were patches of various flowers, especially *Eriogonum*, *Eriodictyon*, *Eriophyllum*, *Lotus* and *Salvia* which were visited by buprestids. Included were *Acmaeodera angelica* (in large numbers), *A. perlanosa*, *A. fenyesi*, *A. hepburni*, *A. acuta*, *A. quadriseriata* and *Anthaxia aeneogaster*. The relatively small numbers of *A. angelica* brought in by the wasps in relation to the large numbers collected from this habitat by staff and students (Table II) is regarded as evidence that it was little used by the wasps as a source of prey.

When the prey of the *Cerceris* are tabulated by individual cells, we find that of 68[5] cells provisioned in 1951, 67 contained buprestids from *Adenostoma*. Of these, 26 contained only *Adeno-*

[4]This observation tends to confirm the statement of Krombein (1953b) that "a certain amount of evidence has accumulated which shows that in some cases the miltogrammine maggots may actively search out and destroy the wasp *egg* before starting to feed on the prey stored for the wasp larva."

[5]One cell contained only *Agrilus blandus*, a species from *Eriogonum* not found in any other cells of the 1951 or 1952 season.

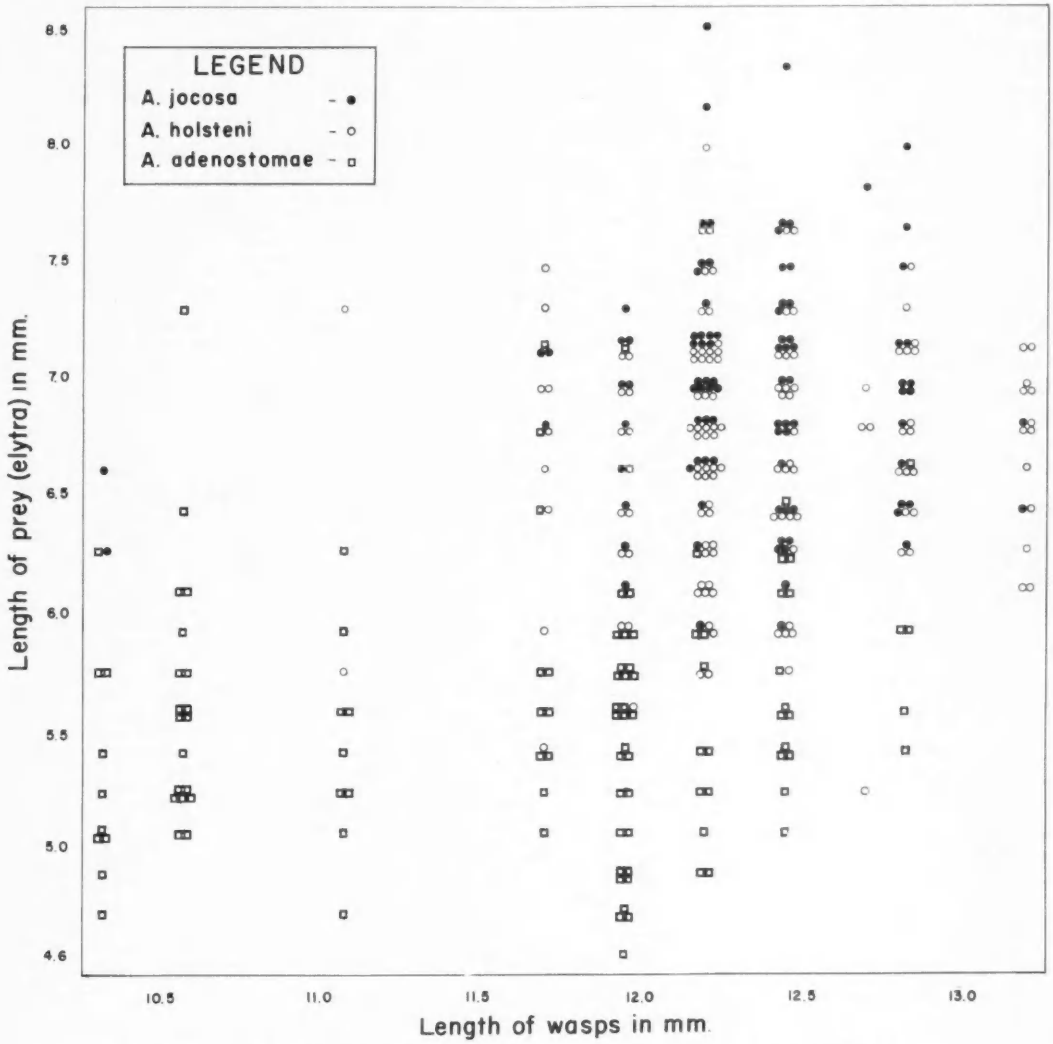

FIG. 3. Relationship of the length of the three species of buprestids associated with *Adenostoma* and the length of the wasps which captured them.

stoma species, 37 also contained *Ceanothus* species, 5 *Quercus* species and 2 *Eriodictyon* species. Thus the Chamise chapparal association appears to have been the preferred habitat for searching and *Adenostoma* the major source of prey. In 1952, of 77 cells examined, 74 contained *Adenostoma* species but only seven cells contained *Adenostoma* forms alone. Sixty-two cells contained *Ceanothus* species, 22 *Quercus* species, 3 *Eriodictyon* types and a few other miscellaneous forms. Although a preference for *Adenostoma* as a source of prey is still evident, the influence of *Ceanothus* appears greater than in the 1951 prey series.

When the prey are tabulated by individual female wasps, the 14 females of the 1951 season were all found to have collected prey from *Adenostoma*. Twelve of these had also worked *Ceanothus*, four *Quercus*, one *Eriodictyon* and two may also have collected from flowers. In the 1952 season, at least 24 of the 25 females had collected from *Adenostoma*, 23 had also visited *Ceanothus*, seven to nine had visited *Quercus*, four *Eriodictyon* and two or three may have captured prey on flowers.

Thus to summarize, in the 1951 season all 14 of the females from the nest site collected prey from *Adenostoma*, these were found distributed

TABLE II

BUPRESTID PREY OF CERCERIS CALIFORNICA CRESSON AT TANBARK FLAT, CALIFORNIA IN 1951 AND 1952

PREY SPECIES	1951 COLLECTIONS[1]		1952 COLLECTIONS[2]		1951 CERCERIS PREY[3]		1952 CERCERIS PREY[4]		LOCAL HABITAT OF BUPRESTIDS
	Number	Percent	Number	Percent	Number	Percent	Number	Percent	
Acmaeodera holsteni	394	17.5	17	2.0	77	18.2	173	24.5	*Adenostoma;* rarely on small flowering plants
adenostomae	77	3.4	38	4.6	116	27.5	130	18.4	*Adenostoma*
jocosa	342	15.2	55	6.6	128	30.3	121	17.2	*Adenostoma*
nexa	20	0.9	4	0.5	22	5.2	79	11.2	*Ceanothus*
dohrni	27	1.2	2	0.2	10	2.4	59	8.4	*Ceanothus*
prorsa	72	3.2	43	5.2	10	2.4	41	5.8	*Ceanothus;* also on small flowering plants
acula	32	1.4	8	1.0	3	0.7	27	3.8	*Quercus;* also on small flowering plants
quadriseriata	25	1.1	47	5.6	2	0.5	18	2.6	Small flowering plants
angelica	548	24.4	356	42.7	11	2.6	15	2.1	Small flowering plants; *Ceanothus*
coquilletti	120	5.3	82	9.8	3	0.7	9	1.3	*Quercus*
dolorosa	39	1.7	21	2.5	6	1.4	7	1.0	*Ceanothus;* also on small flowering plants
sinuata	147	6.5	8	1.0	13	3.1	5	0.7	*Ceanothus*
hepburni	44	2.0	52	6.2	2	0.5	3	0.4	*Quercus;* also on small flowering plants
perlanosa	12	0.5	16	1.9	1	0.2	3	0.4	*Eriodictyon*
fenyesi	85	3.8	24	2.9	2	0.5	2	0.3	*Eriodictyon:* also on small flowering plants
plagiaticauda	1	0.0	7	0.8	—	—	2	0.3	*Arctostaphylos*
gemina	4	0.2	4	0.5	—	—	1	0.1	On ground near small flowers
Chrysobothris deleta	60	2.7	14	1.7	—	—	2	0.3	*Ceanothus*
lucana	154	6.9	8	1.0	2	0.5	1	0.1	*Ceanothus*
Agrilus angelicus	7	0.3	8	1.0	—	—	3	0.4	*Quercus*
blandus	24	1.1	10	1.2	13	3.1	—	—	*Eriogonum*
Anthaxia aeneogaster	12	0.5	10	1.2	1	0.2	4	0.6	*Quercus;* also on small flowering plants
Totals	2,246	...	834	...	422	...	705	...	

[1]Collected by Summer Field Course staff and students by beating shrubs and trees and sweeping flowering plants.
[2]Collected by Summer Field Course staff and students mainly from flowering plants.
[3]Full season.
[4]At mid-season.

through 67 of the 68 cells stored by these females, were found exclusively in 26, and represented 76 percent of all of the buprestids captured. Twelve of these females also collected beetles from *Ceanothus*. These were found in 37 of the 68 cells and represented 18 percent of the total catch. A few females also took prey from *Quercus* and possibly also from other plants.

In 1952, at least 24 of the 25 females had also taken prey from *Adenostoma*. These were distributed through 74 of the 77 cells provisioned but were found exclusively in only seven and represented only 60 percent of all the buprestids captured. Twenty-three of the 25 females had also visited *Ceanothus* and prey from this source was distributed through 62 of the 77 cells and represent 30 percent of the total catch. No cells of either the 1951 or 1952 season were made up exclusively of *Ceanothus* species. Among the few cells from other or uncertain sources one or two may have come exclusively from a single host plant. Thus a few individuals (*viz.*, Table III, Nos. 16, 17) apparently discovered or exploited different habitats from the majority of the other females.

(b) Relation of size of wasps to size of prey.

Within a given habitat, the major factor limiting capture and transport of prey, is apparently the size of the female wasp. This is evident when the prey are grouped by average size of the species (Table III) or arranged by size of individuals within the species (fig. 3). Thus, generally speaking, the largest wasps took greater numbers of the larger species of buprestids as well as the largest individuals within these species. However, these wasps did not completely reject the small buprestids and as a result the range of size of the prey captured was greater than for the smaller females. Since we lack data on the distribution by size of the buprestids actually encountered by the hunting wasps we cannot state whether the range repre-

TABLE III

BUPRESTID PREY BY HOST PLANT OF TWENTY[1] FEMALE CERCERIS, 1952 SEASON

PREY BY HOST PLANT[2]	WASP NUMBER AND TOTAL LENGTH IN MM.																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Adenostoma	13.3	13.0	12.8	12.5	12.5	12.5	12.3	12.3	12.3	12.3	12.0	12.0	12.0	12.0	11.8	11.8	11.8	11.0	10.5	10.3
Acmaeodera jocosa	3	15	1	10	13	8	15	9	7	4	3	3	3	2	2	1				2
Acmaeodera holsteni	17	16	4	15	8	4	20	14	14	10	6	4	3	5	5	4		2		
Acmaeodera adenostomae		5		5	5	5	7	1	2	1	1	1	5	24	4	6	1	9	20	10
Ceanothus																				
Acmaeodera sinuata		1		1	1		1													
Acmaeodera dohrni	3	4	2	2	5	2	13	15	5	3	1					1				
Acmaeodera prorsa	1	2	1		1	3	1			3	1		1			14				
Acmaeodera dolorosa			2			1	1									2				
Acmaeodera angelica	1		1	1			1				1	2	1							
Chrysobothris deleta			1													1				
Chrysobothris lucana		1																		
Acmaeodera nexa	1	7	1	3	1	2	3		2	3			5	18	8	1	16	3	10	9
Quercus																				
Acmaeodera hepburni							1									1				
Acmaeodera coquilletti				1	2	2	1				1									1
Acmaeodera acuta				1												15	7			1
Agrilus angelicus																				2
Anthaxia aeneogaster											1					1	2			
Eriodictyon																				
Acmaeodera fenyesi							1													
Acmaeodera perlanosa							1			1						1				
Arctostaphylos																				
Acmaeodera plagiaticauda									1							1				
Uncertain																				
Acmaeodera quadriseriata	1		1													2	14			
Acmaeodera gemina				1																

[1]Provisions of five females were not included because four had captured less than ten buprestids and there was some question as to whether or not the cells of the fifth were properly associated.

[2]Species arranged in descending order of average size in each host plant group.

sented in the prey of the larger wasps reflects chance alone or a tendency to select the larger beetles.

SUMMARY

Observations on the nesting habits of 25 females of *Cerceris californica* Cresson and the structure and location of the burrows are described. The daily activity pattern of the wasps is recorded as well as the factors which appear to influence this pattern. A mutillid and several sarcophagids are recorded as parasites of *C. californica*. An analysis of the prey stored by the wasps in two seasons revealed that the main factors influencing selection of prey were habitat preferences of the buprestid beetles and a relationship between size of the wasps and size of the prey.

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INFECTION OF COCKROACHES WITH HERPOMYCES (LABOULBENIALES) II. HISTOLOGY AND HISTOPATHOLOGY[1, 2]

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INTRODUCTION

The Laboulbeniales are a group of fungi assigned to the Ascomyceteae. All of the approximately 1500 described species are obligate parasites growing on the cuticle of living insects or mites. Most of the species are described from adult Coleoptera and Diptera, but the 25 species of *Herpomyces* are all found exclusively on cockroaches (Thaster, 1931). We have studied three species in colonies here: *H. stylopygae* Spegazzini on *Blatta orientalis*, *H. ectobiae* Thaxter on *Blattella germanica*, and *H. tricuspidatus* Thaxter on *Blaberus craniifer*. These fungi are largely host specific (Richards and Smith, 1955b). Most of our work has dealt with infections of *H. stylopygae* on oriental cockroaches. In Part I of this series we presented data on the location, maintenance and transmission of the infection, and on the interesting phenomenon of the infection being lost at ecdysis. In Part III we plan to treat host specificity, and in subsequent installments other facets of this host-parasite relationship.

In the present installment, data are presented from a histological examination of the fungi and of infected integuments. Infections of *H. stylopygae* are mostly located on the antennae of oriental cockroaches. About 80% of the specimens in infected colonies have fungi only on the antennae (fig. 1). Others usually have them on both antennae and maxillary palpi. Rarely, a few plants have been seen elsewhere (Richards and Smith, 1955a) but at least 99% of the plants are on antennae. With *H. ectobiae* plants are found, more scattered, over the entire body of german cockroaches, including the wings.

According to the literature the Laboulbeniales are non-pathogenic parasites usually said to cause no deleterious effect on the host. They appear to be worthless for biological control.

MATERIALS AND METHODS

The fungi are maintained in the laboratory without difficulty in infected colonies of the several cockroach species (Richards and Smith, 1955a). Specimens are taken from such colonies whenever desired.

Some of the studies on the fungal cell walls have been done with whole mounts (Richards, 1954), but most of the present paper is based on serial sections. Since cockroaches become fully sclerotized in about two days whereas the fungus requires two weeks for growth, it is obvious that mature plants will be formed only on fully sclerotized cockroaches. But, fortunately, cockroach cuticle is not extremely difficult to section even when fully hardened. Even so, excellent sectioning technique is necessary because the area of haustorial penetration readily fragments and is lost. Apparently the penetrating haustoria make the immediately surrounding cuticle friable. To judge from our experience, we suspect that this difficulty accounts for the negative results reported from sectioned material by Mercier and Poisson (1927).

Short pieces (2–5 mm.) of antennae were fixed in Zenker's formol, Carnoy's fluid, or 5% acetic or propionic acid in 95% ethanol, or pretreated with the argentaffin reagent (Richards, 1951) followed by fixation in 50% ethanol then absolute ethanol. The Carnoy-fixed material was double embedded in celloidin and paraffin, the others were embedded in Tissuemat via benzene. Sections were cut at various thicknesses, 4–6 microns being subsequently found most useful. Most of the illustrations are prepared from 6 micron sections. Mallory's triple connective tissue stain (with or without the Orange G) was found to give excellent differentiation; it was used routinely. In some cases the stain was superimposed on a previous silver deposit from the argentaffin reagent (figs. 16 and 18).

Photographs were commonly made with complementary color filters to accentuate the contrast of desired portions.

CELL WALLS OF THE FUNGAL PLANT

Like ascomycetes in general, the cell walls of *Herpomyces* contain chitin instead of cellulose (Richards, 1954). More interestingly, they show differentiation similar to that of insect cuticle (Richards, 1951). Thus, with Mallory's stain, the walls of *H. ectobiae* are a uniform clear blue (= insect procuticle and endocuticle); the walls of *H. stylopygae* are similarly blue except for the

[1]Paper No. 3268. Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul 1, Minnesota. Accepted for publication, November, 1954. Line cuts and half tones supplied by the authors and were made prior to the change in the format of the ANNALS.

[2]The work described in the present paper was supported under terms of a contract between the office of the Surgeon General, U. S. Army, and the University of Minnesota.

Our sincere thanks are due to Dr. R. K. Benjamin of the Rancho Santa Ana Botanic Garden, Claremont, California for identification of the fungus species, and to him and Dr. L. Shanor of the University of Illinois and Dr. Clyde Christensen of the University of Minnesota for critical reading of the manuscript. Thanks are also due to Dr. L. M. Roth of the Army Quartermaster Laboratories for calling our attention to the paper by Gunn.

shield of the secondary receptacle which stains red distally (= insect mesocuticle) and is amber to black and refractory to staining basally (= insect exocuticle); the lower walls of the receptacle of *H. tricuspidatus* stain blue but walls of the mature perithecia are purplish grading to red staining at the terminal prongs, some of which are amber colored and refractory to staining (the outer wall of the secondary receptacle is also red staining grading to amber and refractory at the extreme base).

The walls of the perithecia show a helical arrangement of micelles more or less similar to those in sporangiophore stalks (Castle, 1953). After treatment in Diaphanol[3], they show between crossed Nicols with a red-wave compensator both yellow and blue in distinct streaks, in the manner to be expected of micelles following a helical path from base to tip of the perithecium.

It has been said (Thaxter, 1896, p. 234; Benjamin and Shanor, 1950) that the gelatinous sheath around the spore persists as a membrane around the entire mature fungal plant. Presumably these statements are meant to imply only that the gelatinous material around a spore dries down to form a thin membrane and that a similar appearing thin membrane can be seen around the outside of mature plants, i.e. that there is a developmenal continuity between the sheath around spores and that around mature plants. Geometric calculations show the material around spores is inadequate to be stretched to form a sheet around the entire plant. In a large female plant of *H. stylopygae* there is approximately 300 x the surface area of a spore. Since the dried coat around a spore is only a small fraction of a micron thick it would have to become impossibly thin to cover 300 x as much area (about 10 x thinner than the thinnest natural membranes known from electron microscopy). Even with the much smaller *Laboulbenia formicarum*, one can calculate from the figures of Benjamin and Shanor that the surface area of the mature female plant is 40–50 x that of a spore.

[3]A saturated solution of chlorine dioxide in 50% acetic acid.

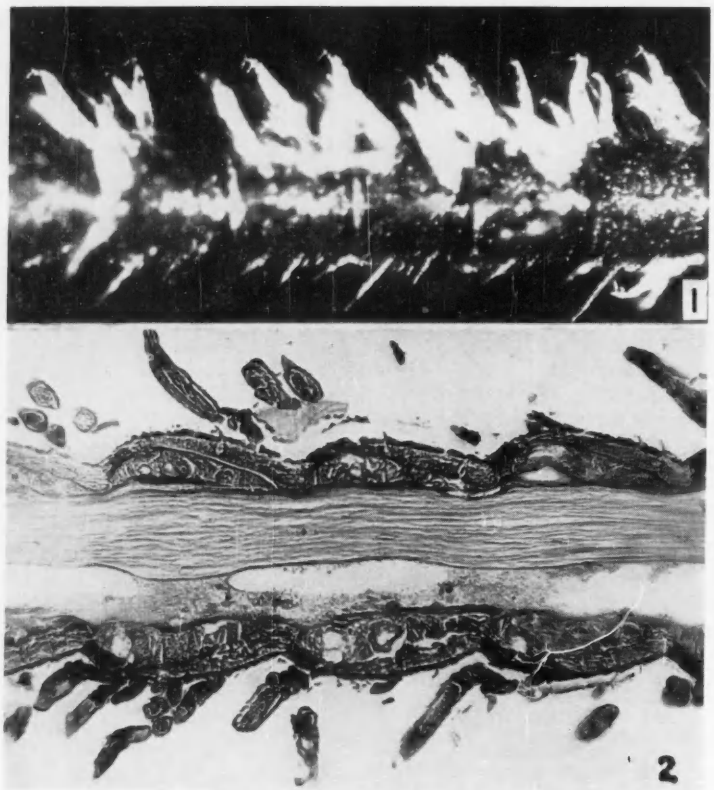


FIG. 1. Six antennal segments of *Blatta orientalis* infected with fifteen plants of *Herpomyces stylopygae*. 90 X. FIG. 2. Longitudinal section of an infected antenna. 150 X.

A distinct surface layer ($< 0.5\,\mu$ thick) of relatively high refractive index and acidophilic staining properties can be seen overlying the basophilic walls in our sections (figs. 5 and 10). Volume considerations necessitate, as stated above, that this be secreted during growth. Neither with phase contrast optics nor with color filters did thin sections ($3\,\mu$) show any trace of a separate pellicle or of filaments extending through the cell walls to the surface layer, such as Thaxter (1896) found in certain species of *Laboulbenia*.

The cells of the spore and of the very young plant are clearly uninucleate (in sections stained with Mallory's this is best seen when using a blue filter). In the older plant, cells of the primary receptacle, of the shield over the secondary receptacle, and seemingly of the elongated cells of the secondary receptacle and of the perithecia are also uninucleate. However, the large basal cells just basal to the perithecia are clearly binucleate (figs. 6–9). These binucleate basal cells of the perithecia are distinctive in another respect, namely they have clear cytoplasmic bridges between the cells (figs. 7–9). These cytoplasmic bridges range in size from what are only slight constrictions in an elongated and twisting cell through moderate sizes (fig. 9) to minute strands (fig. 8) comparable to ones illustrated by Thaxter (1896). Cytoplasmic connections between cells were not seen in any other parts of the plant.

The secondary receptacle is closely appressed to the cuticle of the host (figs. 17). When germination begins on a seta, the mature plant grows around the seta as well as across the antennal surface, thereby further anchoring itself. When no seta is involved it is uncertain whether the plant is held by the haustoria alone or partly by adhesion to the surface of the host (the germinating spore has holdfasts; Richards and Smith, 1955a). Be that as it may, the secondary

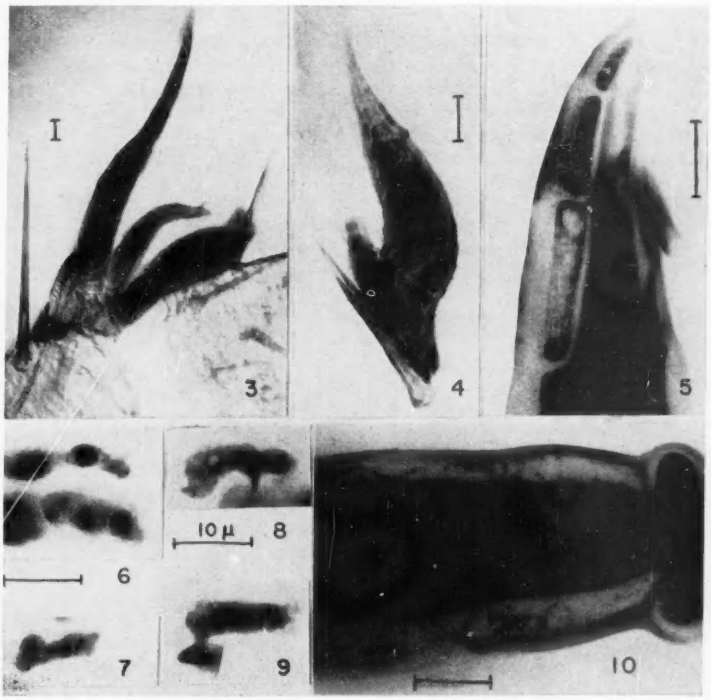


FIG. 3. Lateral view of a single mature female plant of *Herpomyces stylopygae* on antenna of nymph of *Blatta orientalis*. 280 X (Bar 10 μ). FIG. 4. Lateral view of a nearly mature female plant of *H. ectobiae* on antennal seta of *Blattella germanica* (compare FIG. 14D). 670 X (Bar 10 μ). FIG. 5 Longitudinal section of apical ortion of perithecium of *H. stylopygae* showing thin differentiated surface layer. Section 3 μ thick, stained with Mallory's triple, photographed with a green filter. 1150 X (Bar 10 μ). FIGS. 6–9. Section showing binucleate basal cells of perithecium and intercellular cytoplasmic bridges in *H. stylopygae*. Mallory's triple stain, photographed with a blue filter. 1200 X (Bars 10 μ). FIG. 10. Longitudinal section of basal part of perithecium of *H. stylopygae*, primarily to show differentiation of thin surface layer. Section 3 μ thick, stained with Mallory's triple, and photographed with a green filter. 1150 X (Bar 10μ).

receptacle, including the blackened basal portion commonly called the "foot", is entirely on the surface of the host, not embedded in the cuticle.

PENETRATION INTO THE HOST

It has been recognized since early work by Thaxter (1896) that some species have haustoria penetrating into the insect. However, it is commonly stated that such penetration is exceptional. Thaxter said, "In the great majority of instances, however, it is probable that there is no intrusion of any kind from the ordinary form of blackened foot into the substance of the host." Similar statements occur in recent textbooks (probably based on Thaxter's statement). Approximate calculations show that mature female plants of *H. stylopygae* have 3,500–20,000 x the volume of the spore from which they arise. Other species increase from a few hundred times to more than 100,000 x the spore size (Richards and Smith, 1955a). It is obvious that considerable nourishment must be obtained, and it should be equally obvious that such an amount cannot be obtained from a small chunk of insect cuticle at the base of the plant. And, actually, serial sections fail to reveal any digestion of cuticle other than a canal or canals for penetration of the haustorium or haustoria. Further, if species of Laboulbeniales simply lived on the surface of insects, with or without digesting some of the insect's cuticle, one would expect to be able to rear them readily on explanted pieces of cuticle—we have not succeeded in accomplishing this (Richards and Smith, 1955a). We had intended in writing this series of papers to restrict all of our conclusions to apply to the genus *Herpomyces* but on this point we are willing to hazard a generalization. It seems to us almost impossible to imagine species of Laboulbenials growing on the external surface of insects without having haustoria penetrating into the insect for nourishment.

Thaxter (1896) implied that Laboulbeniales might absorb nourishment through the insect's cuticle without penetrating it. Considering the literature of the permeability of insect cuticle (see Richards, 1951) this seems quite impossible unless one postulates that the fungus alters the cuticle in such a way as to destroy its barrier properties at the contact area of fungus and host. This seems so unlikely that it does not warrant discussion until and unless someone can produce evidence that such may occur.

Large haustoria penetrating into the insect have been recorded for a few species by Thaxter (who was so impressed when he saw them that he coined names such as *Rhizomyces* and *Dimeromyces rhizophorus*) and by Chatton and Picard (1909). Minute haustoria have been reported by Thaxter (1908), Colla (1926) and Poisson (1930). One

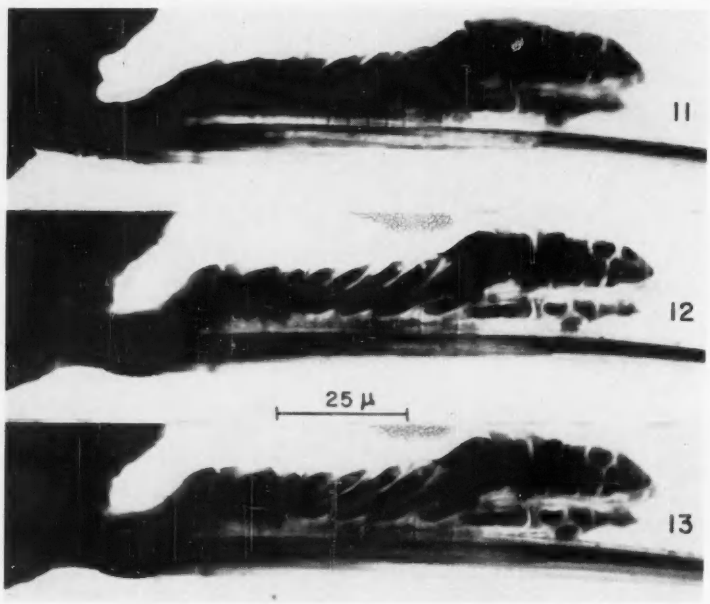


FIG. 11. A growing plant of *Herpomyces stylopygae* on an antennal seta of *Blatta orientalis*. Note haustoria into cytoplasm of seta and the lysis of cytoplasm in the region of haustorial penetration (compare Fig.14C). 780 X. FIG. 12. Slightly different focus on same specimen showing haustoria more apical on the seta. Printed on Kodabromide F-5 for high contrast. FIG. 13. Same negative as preceding but printed on Kodabromide F-2 to show the nearly transparent wall of the seta and the outlines of the cells of the fungal plant.

might well ask why these have not been reported more frequently (Dr. Benjamin tells us that he has seen them "many times"). Possible answers include the fact that they usually do not show in whole mounts because masked by staining of the epidermal cells of the host, that they are almost always broken off when the fungus is removed from the cuticle (with or without an adhering fragment of cuticle), that in sections the region of penetration is likely to be lost due to its friability, and that the minute haustoria are almost impossible to distinguish from the pore canals in insect cuticle (these pore canals do not occur in setal walls and hence the haustoria are easy to distinguish there, Figs. 11–13).

THE HAUSTORIA OF HERPOMYCES STYLOPYGAE

Three types of haustoria can be recognized with this species: (1) Fine filamentous strands from cells of the secondary receptacle of germinating plants into setal shafts (figs. 11–14), as already described by Thaxter (1908), likely from plants belonging to this species. These minute haustoria measure about 0.3 μ in diameter but are probably of the order of 0.1 μ in diameter[4]. Presumably similar minute haustoria are formed by secondary receptacle cells of plants germinating on the general body wall but it would be extremely difficult to distinguish minute haustoria among a virtual forest of pore canals. We have not attempted to do so[5].

(2) Relatively small, distinctly tubular haustoria of 1.5–2 μ diameter associated with male plants and thought to originate from them. These are large enough to permit unquestionable recognition as belonging to the fungus (fig. 16). Within the epidermal cell layer of the cockroach these expand into a haustorial bulb.

(3) Relatively large, less sharply delimited haustoria of 2–5 μ diameter associated with female plants and thought to be characteristic of them (figs. 17–23). These are easily distinguished in sections when penetrating through a continuous sheet of cuticle but may be difficult to distinguish when, as commonly occurs, penetration is effected through a setal socket unless the section is heavily stained (then haustorium blue in the red cytoplasm of the trichogen cell of the seta fig. 19). This type also expands into a large bulb in the epidermal cell layer.

When male and female plants grow as a pair together, both types 2 and 3 are found, sometimes penetrating through a single perforation (fig. 16).

When a spore of *H. stylopygae* germinates on a seta it divides to the 4-cell stage, develops holdfasts (Richards and Smith, 1955a), and then the cells begin to differentiate. The basal end becomes additionally attached to the seta by the penetration into the setal shaft of a minute haus-

[4]A filament of 0.1 μ diameter seen by its diffraction lines would measure about 0.3 μ in white light. The value of approximately 0.1 μ is supported by the fact that measurements with an electron microscope show that the pore canals of cockroach cuticle are about 0.1 μ in diameter and coiled into a helix averaging 0.25 μ diameter (Richards, 1951). The minute haustoria are clearly thinner than the pore canal helices, and seem to be about the same diameter as the pore canal.

[5]It is by no means clear from his paper whether Poisson (1930) saw haustoria or misidentified pore canals.

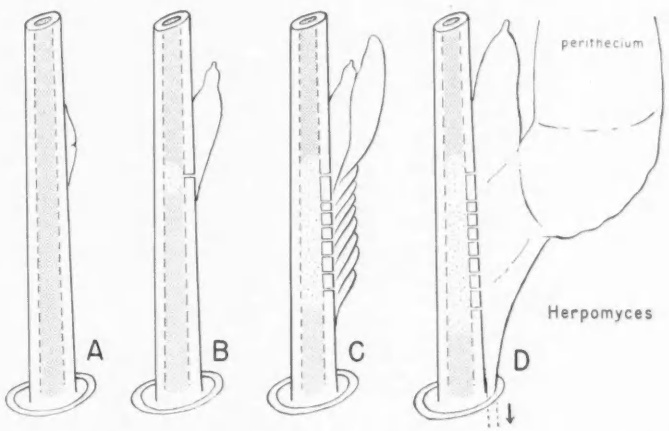


FIG. 14. Series of diagrams showing germination of *Herpomyces* spores on setae. *A*. Spore in 2-cell stage. *B*. Early stage in differentiation with single haustorium penetrating into setal shaft. *C*. Subsequent development, with formation of row of haustoria and with further lysis of setal cytoplasm, as occurs when spores of *H. stylopygae* germinate on setae (compare Figs. 11–13). *D*. Subsequent development, with penetration of large haustorium through setal socket and formation of perithecium. Fig. D is typical of *H. ectobiae* (compare Fig. 4); in *H. stylopygae* growth involves a greater development across the surface of the antenna at the base of the seta to give an appearance such as figure 3 but with a seta in the middle of the plant.

torium from the basal cell (fig. 14B). As differentiation proceeds, the secondary receptacle extends down the seta with each cell (except at the extreme growing end) having a similar haustorium penetrating into the setal shaft (fig. 14C, also 11–13). With further growth the thallus reaches the base of the seta and one of the larger types of rhizoids penetrates around the setal base (fig. 14D).

When a spore germinates on the surface of the body wall the first stages are presumably similar but have not been demonstrated. By the time the female plant is developing perithecia, a large haustorial tube is found penetrating a perforation which it fits snugly. Beneath the cuticle this expands into a bulb which may be spherical but which with increased growth usually becomes a flattened spheroid (fig. 15). This large haustorium appears to be produced by a single cell of the secondary receptacle. In numerous cases we have been able to trace these haustoria into single large cells (fig. 21). An interesting point is that the haustoria are basophilic and stain a light blue with Mallory's stain; after extending into a cell of the secondary receptacle the stainability changes either gradually or abruptly to acidophilic and the end of the cell containing the nucleus stains with the acid fuchsin of Mallory's stain, as do all of the protoplasts except the haustorial prolongation.

The haustorial bulbs displace their volume in the epidermal cell layer of the host but are commonly not sharply delimited from the epidermal cells despite the fact that the haustoria stain lightly blue while the epidermal cells are red (fig. 17). When a fixative which causes considerable shrinkage is used the haustorial bulb may be quite clear (fig. 19), or clear near the cockroach's cuticle and losing its identity in the epidermal cells at a lower level (fig. 20).

The haustoria are limited to the epidermal cell layer. They may cause the basement membrane of the integument to bulge inwards (fig. 22) but were never seen to penetrate this limiting membrane of the integument. The common flattening of the bulb and distension of the basement membrane suggest that the haustorium is incapable of penetrating the barrier into the body cavity (blood cavity).

The haustorial bulbs are commonly 30–50 μ in diameter with some of the larger ones reaching 100 μ diameter and 40–50 μ depth (fig. 22). In volume, then, they are mostly 25,000–60,000 cubic micra with the largest attaining 175,000 cubic micra. In other words they represent 20–30% of the total volume of the mature plant (Richards and Smith, 1955a). However, they seldom displace an area of cuticle-epidermis interface equivalent to the diameter of the bulb because the swelling tends to be centrally or basally located in the epidermal layer (fig. 15). There usually appears to be some epidermal cytoplasm over most of the cuticle-epidermis interface except, of course, for the point of penetration through the cuticle.

Incidentally, the haustorial tubes through the cuticle are argentophilic and are demarcated by silver granules after treatment with amoniacal silver nitrate (figs. 16 and 18), just like the surface of the external portion of the plant (Richards, 1954). In our preparations the haustorial bulb appears to be negative to this reaction but since

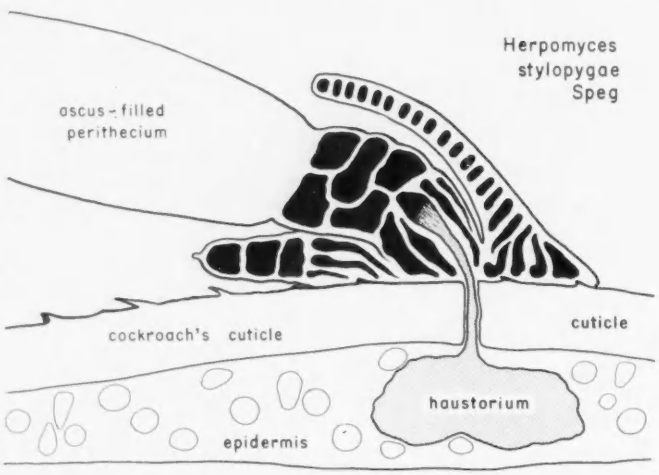
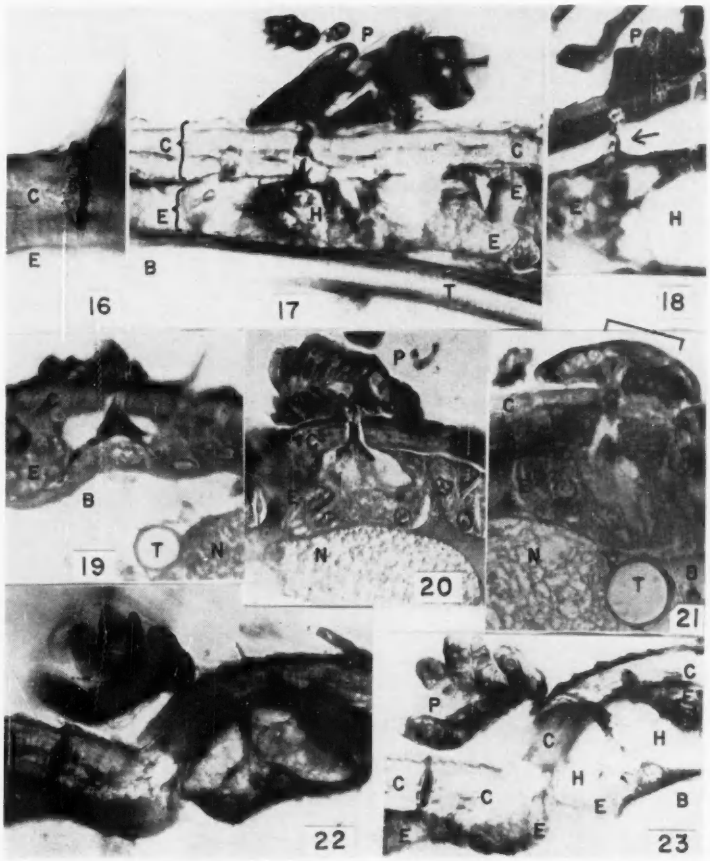


FIG. 15. Diagram of the relation between a mature plant of *H. stylopygae* and the integument of *Blatta orientalis* (compare Fig. 17) when germination is on the surface of the antenna. When germination of this species begins on a seta, the sequence of events is from the condition diagrammed in Fig. 14C to that shown in this diagram with the modification that the plant would be partly appressed to a seta and the haustorium would penetrate through a setal socket (as in Fig. 19).

the reagent was only applied externally to the antenna prior to histological fixation there is no assurance that it penetrated to the bulb.

It has been suggested (*e.g.*, Lilly and Barnett, 1951, p. 374) that the penetration of haustoria is brought about by mechanical pressure because enzymes capable of digesting a hole have not been demonstrated. Histological evidence does not support this suggestion for *Herpomyces*. The haustorial tube fits snugly into its perforation through the cuticle (figs. 17 and 23) unless fixatives causing shrinkage were used or unless penetration is via a setal socket (fig. 19). No distortion of the cuticular laminae of the host's



FIGS. 16–23. Sections of antennae of *Blatta orientalis* infected with *Herpomyces stylopygae*. All stained with Mallory's triple connective tissue stain.

FIG. 16. Section of cuticle of antenna treated with ammoniacal silver nitrate, fixed, sectioned and then stained with Mallory's. Note large cavity with argentophile granules (haustorium of female plant) and smaller blue staining tube (haustorium of male plant). 850 X. FIG. 17. Longitudinal section of antenna photographed with a red filter to minimize the cuticle and the red-staining epidermal cells and to bring out in contrast the blue-staining plant and its haustorium. 550 X. FIG. 18. Section of an antenna treated with amoniacal silver nitrate (as Fig. 16) at a point where the epidermis has become separated from the cuticle during sectioning. Note the argentophile granules in the unbroken haustorium traversing the space between the cuticle and epidermis. 300 X. FIG. 19. Cross section of antenna fixed in Carnoy's fluid and showing the shrunken haustorium with root-like processes. Penetration via a setal socket. 550 X. FIG. 20. Cross section of antenna fixed in Carnoy's fluid and showing shrunken haustorium which loses its identity among the epidermal cells when only shortly past the cuticle. 550 X. FIG. 21. Cross section of antenna showing that haustorium originates from a single large cell (bracket) of the secondary receptacle of the plant. 550 X. FIG. 22. Longitudinal section of antenna photographed with a green filter to bring out internal detail of the haustorial bulb. 360 X. FIG. 23. Same negative as preceding but printed lightly on high contrast paper (F-5) to bring out the haustorial tube penetrating through the cuticle. 360 X.

Legend: *B* = body cavity or blood; *C* = cuticle; *E* = epidermis; *H* = bulb of haustorium; *N* = nerve; *P* = thallus of plant; *T* = trachea.

cuticle is visible either by phase contrast optics or in stained sections,[6] and no interference with the strong birefringence of setae is seen in polarized light. It does not seem to us reasonable that haustoria could drill such clean holes through hard insect cuticle by pressure alone. We therefore suggest that the penetration of *Herpomyces* haustoria is accomplished by enzyme action.

If penetration is accomplished by enzyme action, then it follows that the fungus must have an enzyme system capable of digesting insect epicuticle, exocuticle and endocuticle, i.e., it must have a more powerful set of enzymes than the insect uses in molting. It is already known that many bacteria can digest hardened insect cuticles and there is some evidence that certain fungi can also do so (Richards, 1951). Further, the enzymes cannot be secreted freely or in excess because if they were the perforation would be larger than the haustorial tube and not fit it snugly. Presumably the enzymes would have to be bound to the haustorial surface, perhaps only to the tip thereof.

THE HAUSTORIA OF OTHER HERPOMYCES spp.

A few sets of serial sections were prepared of antennae and legs of *Blattella germanica* infected with *H. ectobiae*. These showed similar pictures to the infections of *H. stylopygae*, except that *H. ectobiae* seems always to germinate on setae and to penetrate through a setal socket when it reaches the general body wall. Correlated with its smaller size it has a smaller haustorial bulb in the insect's epidermis. Of more interest, plants growing on the femora and tibia of legs also penetrate at setal bases and show haustoria in the epidermis which differ in no important respect (correlated with the thinner epidermal cell layer in legs the haustorial bulbs are more flattened than those seen in sections of antennae). The histology of the infection, then, is similar for plants growing on different parts of the body.

A few sets of serial sections of antennae of *Blaberus craniifer* infected with *H. tricuspidatus* were likewise similar. In this giant cockroach, the epidermal cell layer is thicker. Correlated with this the haustorial bulbs seen were consistently nearly spherical.

From both developmental and comparative data it appears that the shape of the haustorial bulb is not a specific characteristic in *Herpomyces* but only the by-product of pressure and space to grow in.

PATHOLOGY OF THE INFECTION

As stated in the preceding section, a single haustorial bulb of *H. stylopygae* may occupy 25,000 to 175,000 cubic micra of space in the epidermal cell layer of the cockroach's antenna. In heavy infections as much as 10% of the total volume of the epidermis may be occupied by these bulbs; in some antennal segments the value may rise to 20–25% of the epidermal volume. Whether this involves displacement of part of the epidermis or distension of the epidermal volume was not determined. Probably both are involved because sometimes the basement membrane of the integument can be seen to be bulged into the body cavity, (fig. 25) and, commonly, nearly naked epidermal nuclei can be seen more or less engulfed in the haustorium (fig. 22) or the haustorium appearing to grade off into the epidermal cells (figs. 20–21). In setae, the region of haustorial penetration stains very lightly and diffusely suggesting lysis of the cytoplasm of this portion (figs. 11–14). However it is doubtful that the cytoplasm in the setal shaft has any important function after it finishes forming the setal cuticle.

Clearly these species of *Herpomyces* are obligate parasites (Richards and Smith, 1955a) that produce characteristic alterations in the epidermis. Whether or not the infections are referred to as a disease depends on whether or not one arbitrarily defines a disease as pathogenic. Clearly the infections do cause a dermatitis, and the characteristic appearance of the epidermis can be called the histopathology associated with the infection.

But is there any pathogenicity or debilitation? We have seen none. Although precise quantitative determinations have not been made, we have observed that heavily infected cockroaches appear fully active in the colonies, they can run at approximately the same speed, they reproduce normally, and they do not appear to die prematurely. This is equally true for *Blatta* and *Blaberus* where the infections are mostly on antennae, and for *Blattella* where the infection may be all over the body (but is less dense and may not involve any more fungal plants than a heavy antennal infection on *Blatta*).

The one reference we have found in the literature to a deleterious effect is the report by Gunn (1938) that such infections make the reactions of oriental cockroaches to humidity erratic.[7] This is quite reasonable and may well involve other senses. Haustorial tubes penetrating via setal sockets go through the trichogen-tormogen cell complex, and haustorial bulbs in the epidermis can press on or even displace other types of sensilla. However, insects possess such a large number of sensilla that the result may well be

[6] This point does not show clearly in any of the illustrations because the photography has been done to accentuate the haustoria and minimize details of the cuticle.

[7] Gunn's material was identified as "*Stigmatomyces* sp." This is an old generic name. As currently restricted by taxonomists, the genus *Stigmatomyces* contains only species found on Diptera and Coleoptera. All species found on cockroaches are now placed in the genus *Herpomyces*. Probably Gunn had the same species we have worked with (*H. stylopygae* Speg.) on his oriental cockroaches.

more distressing to the sensory physiologist than to the insect.

Cockroach nymphs lose the infection completely at ecdysis, the external portions of the plant being shed with the exuvia (Richards and Smith, 1955a). Obviously the haustoria left behind in the epidermis do not regenerate the infection. We were unable to locate any nuclei in the haustoria except occasionally nuclei questionably within the edge of the haustorial bulb, gigantic in relation to nuclei of the fungal thallus, and indistinguishable from normal epidermal nuclei (surely these belong to the cockroach). If the haustoria are really anucleate, as we think they are, they would not be expected to be capable of regeneration. But, of course, any of several other factors could prevent regeneration.

Finally, sections were prepared of previously infected nymphs of *B. orientalis* at one and two week intervals after they had lost their infection by molting, and of nymphs of *B. germanica* about one week after molting. These showed mostly normal histology in the integument. Although the sections were heavily stained, no haustoria were located. However, in a few places large "vacuoles" were seen in the epidermal layer. These "vacuoles" appeared empty and were not connected to the cuticle, but they did appear similar to photographs of haustoria taken without complementary color filters (see *H* in fig. 18). It seems to us likely that these "vacuoles" represent degenerating haustoria or the space left by degeneration of haustoria. Whether this interpretation is correct or not, no typical haustoria were found, and the integument had at least largely recovered from the infection.

SUMMARY

1. The cell wall of parasitic fungi of the genus *Herpomyces* shows histochemical differentiation similar to that seen in sclerotization of insect cuticle.

2. This group of fungi may increase in volume many thousands of times and hence must derive considerable nourishment from the insect host.

3. Three types of haustoria from the fungus are described as penetrating the cockroach's cuticle and entering the underlying cells.

4. Histological data are presented favoring the suggestion that penetration of the cuticle is mediated by enzyme action rather than by pressure.

5. Cockroach nymphs may recover from the infection completely by shedding the plants at ecdysis but adults keep the infection until they die.

6. The infection of cockroaches with *Herpomyces* gives a dermatitis with characteristic histopathology. However there is no evidence of pathogenicity.

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HOST-PARASITE RELATIONS IN AGAPEMA PUPAE (LEPIDOPTERA, SATURNIIDAE)

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INTRODUCTION

In diapausing pupae of some saturniid moths, carbon dioxide is given off in brief "bursts" alternating with long periods in which the release rate is much lower (for literature see Buck and Keister, 1955). In studying this phenomenon some incidental observations were made which appear to have interesting implications in regard to host-parasite relations during development, and which, it is hoped, will have heuristic value. The presentation has benefited greatly from suggestions of Drs. Raimon Beard, Dietrich Bodenstein, Leigh Chadwick and Curtis Sabrosky.

The observations were made on diapausing *Agapema galbina* (Clemens) pupae, of which males weigh about 800 mg. and females 1200 mg. Respiration was measured by Warburg's direct method at 25° C. The pupae were otherwise kept at 20–25° C.

RESULTS

1. *Location, identification and incidence of parasites.* Parasitized *Agapema* pupae have one (or, exceptionally, two) minute, jet-black, nipple-shaped, shiny papilla protruding above the body surface. The papilla seems to have an axial pore and looks as if composed of solidified exudate. Papillae were found in segments from head to fifth abdominal, and in all quadrants. About half were close to stigmata, the thoracic, first abdominal and second abdominal being the most commonly affected. Of papillae not close to stigmata nearly all were on head and thorax. In four samples of pupae totaling 197 individuals and containing almost equal numbers of males and females, 21% had papillae. Of the parasitized pupae, 61% were females.

The parasite itself is not in evidence until it breaks out through the body wall of the host pupa as a dipterous maggot weighing up to 190 mg. By this time it is apparently mature, since it pupates within 24 hours. After a further period of about 3 weeks at 25° the parasite pupa gives up a large gray tachinid fly. This was kindly identified by Dr. Sabrosky as an undescribed species of *Phorocera* near *floridensis* Tus.

2. *Development of the parasite.* Parasitized *Agapema* pupae afford few clues to the development and activities of the parasite. Most of the hosts showed completely normal respiration, including the usual carbon dioxide bursts, throughout several months, and a few specimens continued through a second year, as do occasional normal pupae. Several such quiescent pupae were dissected, and in each of them the parasite was found as a minute larva, something over a millimeter long, partially enclosed in a black sclerotized envelope or capsule which was immovably attached to the inside of the host pupal wall close to the position of the papilla on the outside surface. The capsule, which covered the posterior two-thirds of the larval body, is perhaps analogous to the "tracheal funnel" formed by many host insects in response to irritation by the parasite (cf. Clausen, 1940; Beard, 1942). It appears from the above observations that the parasite passes a long period in a sessile, inactive stage involving little or no injury to the host. From what is known about other species of *Phorocera* and tachinids in general it is likely that this stage is the first instar, which had entered and induced funnel formation while the host was in the caterpillar stage.

About two weeks before the emergence of the mature parasite maggot, carbon dioxide burst production ceases in the host + parasite unit, and respiratory rate begins to rise. Three pupae were dissected during this period in an attempt to correlate these changes in the host with developmental stage of the parasite. In two of these, which were ostensibly respiring at about 15 times the diapause level (and with no bursts), but in which no heartbeat was visible and in which no response was made to mechanical stimulation, the parasites were found as practically mature maggots of 190 mg., actively moving about within the eviscerated pupal shell. The third host, which still flexed its abdomen in response to mechanical stimulation, and in which heartbeat was visible, but in which oxygen uptake had risen to about 8 times the level of diapausing batchmates, yielded a parasite of intermediate stage. This maggot, much larger than in the sessile stage but still immature, was found near the funnel, but not within or attached to it. After being weighed (34 mg.) and having its oxygen uptake measured, this maggot was returned to the host. Here it grew for an additional 5 days and then emerged as a mature larva of 177 mg. On the day following the restoration of the parasite the host was still able to wiggle its abdomen.

The failure to find any but sessile parasites in pupae with normal respiration, and the finding of only free and growing maggots in pupae with

Accepted for publication, May 25, 1955.

abnormal respiration (for diapause), suggest that the cessation of carbon dioxide burst production marks the rather sudden beginning of active development of the parasite—a development confined to the brief period of two weeks, and continuing up to the time the maggot emerges. The observed fourfold weight increase during the last five days of development—a steep part of the usual logarithmic growth curve—would be compatible with a two week growth cycle and with known development times in some other tachinids. Beard (1940), for example, observed an 11-day cycle in *Trichopoda pennipes* in the laboratory at 26°, and 16 days in the field.

3. *The respiration of the parasite.* The minute size of the sessile stage of the parasite indicates that its respiration could represent no significant fraction of the over-all gas exchange of the host + parasite unit. This expectation was supported by two experiments in which the external papilla was sealed with plastic adhesive for 7 hours without producing any detectible effect on the usual discontinuous pupal CO_2 release. (In one test a gas bubble appeared in the adhesive above the papilla, which may indicate that the axial pore is patent.) The 34 mg. intermediate stage maggot, however, proved to have an oxygen uptake rate 40% of that of the entire host + parasite unit, which, it will be remembered, was itself 8 times the normal diapause level. The respiration of the full-grown maggot was still higher, accounting for practically all the respiration of the host + parasite unit. Though the respiratory rates of the active larvae are thus of the order of 100 times that of the normal diapausing host pupa on a weight basis, they merely reflect the metabolic contrast between active and diapausing tissues and are not unusual on an absolute basis (1 μ L/mg./hr.). On the other hand the rates do indicate that an ample supply of O_2 must be available to the parasite.

It seems to be generally believed that life within the host body confronts a parasite with special respiratory problems. In insects, specifically, the "tracheal funnel" is ordinarily regarded as an adaptation for supplying atmospheric air to the parasite, and there have been described many other remarkable specializations which permit the parasite to extract oxygen directly from tracheal trunks of the host (cf. Keilin, 1944). In the *Phorocera—Agapema* association, however, the funnel involved with the sessile stage of the parasite did not have any structural connection with the host tracheal system. Moreover, no evidence was found that the free, developing parasite ever utilizes, even temporarily, gas from host tracheae, nor is the maggot provided with any of the specialized perispiracular spines or hooks used by some tachinids for tapping host tracheae. It seems in fact clear from the disproportion in size between parasite and host that the very complete evisceration of the latter could only be accomplished by a maggot free to wander through the host's body. Furthermore, it would be expected that as soon as any tracheae were damaged by the feeding maggot they would fill with pupal blood and be no longer capable of conducting air inward.

Nevertheless, it seems highly unlikely that the large active parasite larvae can subsist via cutaneous respiration, particularly in view of the facts (a) that one mature maggot which emerged while the host was actually in the respirometer flask spent two hours swimming in 5.5% sulphuric acid yet survived to pupate and produce a normal fly—a strong tribute to the impenetrability of the cuticle and one which suggests that cutaneous respiration would not be efficient, and (b) that in mature *Calliphora* and *Phormia* larvae, which are morphologically very similar to the *Phorocera* larva, cutaneous respiration normally amounts to less than 5% of the total (Fraenkel and Herford, 1938; Buck and Keister, 1953). Accordingly, this suggests that as the growing maggot consumes the viscera of the host pupa, atmospheric air enters, perhaps through the funnel, into the increasing space formerly occupied by the tissues which have been completely metabolized, and by evaporated water. This would keep the foraging maggot in direct contact with a gas phase and permit a normal sort of trans-spiracular respiratory exchange. Such a gas space is observed during dissection of pupae containing growing parasites, and in truth seems required by the fact that the pupal body does not change dimensionally during the period when something like 1000 mg. of *Agapema* is converted into 190 mg. of *Phorocera*.

4. *The respiration of the host.* The data on the host + parasite unit already presented show that host respiration is normal up to the time the parasite begins active development, and is reduced to zero by the time the parasite is mature. For intermediate stages it is difficult to get a reliable value for pupal respiration *per se* by testing the pupal remains separately because the pupal blood, once exposed, undergoes an active oxidation. However, by subtracting the oxygen uptake of the 34 mg. maggot from that of the host + parasite unit it appears that the respiration of the host pupa had increased to nearly 5 times its diapause level on what would be the 9th day of a two week development cycle of the parasite. As we shall see, this has important implications.

DISCUSSION

Though our observations are incomplete in many respects they may perhaps justify some speculation upon the integration of host and parasite life cycles. The observation of greatest theoretical interest is the increase in metabolic rate of the host pupa which occurs during the period when the parasite's metabolism is like-

wise rising. The exclusive and severe limitation of these increases to the same short time period argues strongly for their causal interdependence. One possible type of dependence is suggested by the following considerations: (a) For the host the increase occurs after a long period of diapause. (b) For the parasite the increase terminates a diapause-like period of inactivity which may have lasted many months. (c) The normal breaking of diapause in unparasitized *Agapema* pupae is invariably accompanied by increased metabolic rate and disappearance of carbon dioxide burst production (Punt, 1950; Schneiderman and Williams, 1955). There thus exists the possibility that the final two weeks of association involves a breaking of diapause in both host and parasite. If this were true, the synchrony of events would seem almost to require that the breaking of diapause in one of the members of the host + parasite unit also trigger the breaking of diapause in the other.

Among circumstances which might be capable of stimulating metabolism in both host and parasite, at least two major possibilities exist. One is that during the long quiet period the host blood contains a substance, produced by either host or parasite, which inhibits the development of the other member of the unit, and that when diapause ends for the producing member the substance is no longer produced or active. As a specific example, it could well be that the high carbon dioxide content of the *Agapema* pupal blood inhibits the development of the parasite until the host breaks diapause and no longer impounds CO_2. The second possibility is hormone action, in which the diapause-breaking hormone of, say, the host, also breaks the (assumed) diapause of the parasite. Although Beard (1940) presented evidence that host hormone is not involved in stimulating the development of the *Trichopoda* larva, which begins only when the host *Anasa* undergoes its final nymphal molt, we favor a hormonal trigger for the *Agapema-Phorocera* association for the following reasons: First, because of the apparent ability of the insect prothoracic gland hormone to initiate development in a variety of stages and in different orders of insects (Williams, 1954). Second, because parasitism by *Phorocera* is supposed to start with the first stage maggot entering while the host is still in the larval stage (Clausen, 1940). There would thus be a considerable period, probably of some days, during which there would be no retention of carbon dioxide. Third, because somewhat similar instances of possible hormonal relation between host and parasite have been described for various syrphids parasitized by ichneumonids (Schneider, 1950). In one instance the first stage parasite does not start feeding until the host forms its puparium, and the activation factor can be shown to reside in the host's hemolymph. Smith and Langston (1953) reported overwintering tachinid first instars in diapausing moth pupae, but did not consider either the cause of cycle synchrony or the triggering of break of diapause.

Teleologically it would be expected that it is the host's hormone which breaks the parasite's diapause, rather than the reverse, since it would be disadvantageous for the parasite to emerge at inclement seasons and/or in the absence of potential host larvae. Most of the data provide no conclusive evidence on this point. Thus the parasites normally emerge during the summer months near the usual time of emergence of adult *Agapema* moths from unparasitized pupae. Likewise the occasional instances of parasitized pupae which skip the usual emergence time and overwinter twice are compatible with either possibility. Triggering of both host and parasite development by host hormone is, however, strongly indicated by the behavior of one large shipment of pupae in which all the unparasitized ones broke diapause prematurely and emerged in January and February, and in which all the parasites also emerged at that time.

SUMMARY

Maggots of the dipterous genus *Phorocera* are found in about 20% of the pupae of the saturniid moth *Agapema galbina*. Data are given about the site and anatomical nature of the infestation and about the respiration of host and parasite. The evidence suggests that the developing parasite utilizes normal trans-spiracular respiration from an air space within the host pupa, the space growing as evisceration proceeds, and it is conceivable that atmospheric air may enter this space via the "funnel" formed by the host at the original site of entry of the parasite.

From evidence that (a) the parasite remains dormant and encapsulated for many months without affecting the metabolic rate or cyclic carbon dioxide release of the host, (b) host and parasite metabolism both increase during and only during the last two weeks of their association, and (c) actively growing and feeding parasites are found only during this last period, it is speculatively proposed that the parasite is aroused from its diapause by the diapause-breaking hormone of the host, the two life cycles being thereby synchronized.

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BIOLOGY OF ANCISTROCERUS ANTILOPE (PANZER) (HYMENOPTERA, VESPIDAE) IN TRAP-NESTS IN WISCONSIN

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An opportunity was taken to study the nesting biology of *Ancistrocerous* wasps when they were found utilizing trap-nests which had been placed in the field for research primarily with Megachilidae. Most of the trap-nests were located in northern Wisconsin at the Ashland Branch Experiment Station or localities not more than 25 miles distant from the station. This report includes studies which were made during 1952, 1953 and 1954.

METHODS

Two types of trap-nests were used. A domicile-type was constructed by bolting several ¾″ x 8″ x 6″ boards together and drilling holes across the grain at the interfaces. The holes were 6.25 mm. (1¼ in.) and 7.8 mm. (5/16 in.) in diameter drilled to a depth of about 150 mm. (6 in.). About 2 dozen holes were drilled in each domicile, the holes being staggered from opposite ends. The blocks were opened for an examination of the individual borings by removing the bolts and separating the boards. After the records were obtained or the cell contents were removed for rearing studies, the boards were re-assembled and again placed in the field. This type of trap-nest has the advantage of being continuously available for nest construction at permanent stations, and the boards can be opened and closed for examination of nests without greatly disturbing or injuring the contents.

The second type of trap-nest was made from an 8-inch length of sumac stem. The soft pith of the stem was cleared out with a drill to a depth of about 6 inches. Usually three or four stems with 6.25 mm. holes and three or four stems with 7.8 mm. holes were wired together in a bundle. The individual stems which were occupied by the wasps were split open in order to obtain data. This style of trap-nest utilizes native material, is easily produced, and is inexpensive, but once the stems are split they are discarded. Sumac bundles are probably best used for surveys and to obtain specimens for laboratory rearing since only the sticks containing nests need be brought back from field stations.

Both types of trap-nests were hung at about head height in trees or large shrubs with the borings in a horizontal position or with the openings tilted slightly downward. The nests were located at different ecological habitats, including roadsides, open woodlots, margins of windbreaks and clearings. The vegetation in these habitats in northern Wisconsin is predominately deciduous in character.

The two different types of trap-nests used in this study are illustrated in fig. 1. A view of a domicile-type opened for inspection of a nest is shown in fig. 2.

It should be mentioned that some of the holes in the domiciles were enlarged to fit 8, 9 and 10 mm. glass tubes (outside diameter) which were slipped into the holes. It was hoped that the progress of cell construction and the subsequent development of the insects could be followed by examining the glass tubes pulled out of the

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Accepted for publication, Jan. 6, 1955.

holes. Although glass tubes were acceptable to the wasps for nest construction, the technique was found to be impractical, largely because of a problem of excessive moisture, mold, and consequent insect mortality. The use of this technique has therefore been discontinued almost entirely.

Many of the data were obtained by removing the insects from the nests and rearing them in the laboratory. The contents of cells were transferred individually to 25 x 95 mm. glass vials. Each vial had about 25 mm. of cellucotton in the bottom, in which a depression similar to a cell was punched to receive the contents of the cell. A drop of water was added to the cellucotton in order to prevent desiccation, and the vials were corked. Careful attention was given to numbering the specimens serially, so that the reared specimens could be associated with cells in the original nests. Specimens ranging in development from eggs to pupa all were reared to adults successfully in the vials. The method was found to be unsatisfactory only in instances where too much water had been added to the cellucotton, since this inadvertently caused a growth of molds and resulted in insect mortality.

FIG. 1. Trap nest used for wasps and bees in Wisconsin. The domicile-type (above) can be opened by removing bolts which hold the boards together. The sumac stems (below) are bundled together with wire. Burrow holes are commonly 6.25 mm. (¼ in.) or 7.8 mm. (5/16 in.) in diameter.

RESULTS

Over a three-year period the specimens of *Ancistrocerus* obtained from the trap-nests were 79% *antilope* (Panzer), 16% *catskill albophaleratus* (Sauss.) and 5% *tigris* (Sauss.). The percentage distribution of nests occupied by each species was 87% *antilope*, 10% *catskill albophaleratus* and 3% *tigris*. Since *antilope* constituted the majority of specimens and more data are needed regarding the other species, the following discussion is restricted entirely to *antilope*.

It is coincidental that Cooper (1953) also has discussed the nesting biology of *antilope* and that many of his data were obtained with a trap-nest technique. The authors wish to express sincere appreciation to Dr. Cooper for his helpful determination of *Ancistrocerous* specimens, and other kind favors extended during the progress of our independent study.

Records relating to finished nests are presented in Table I. A finished nest consists of a linear series of cells, a vestibule cell and a terminal plug. The partitions separating the cells and the terminal plug are made of clay. The thickness of the partitions is variable, range 0.5–3.5 mm. Double partitions are occasionally found. The terminal plugs are thicker than partitions, and vary from 1 to 8 mm. in thickness. The terminal plug almost always is built up in successive layers of clay. In some nests there may be a mixture of empty and provisioned cells. An empty cell does not appear to be consistently different from a provisioned cell in its construction. Table I shows that considerable variation exists with respect to the size and number of cells, the distribution of provisioned and empty cells and the sex ratios of wasps in the nests. In long series the first cells contain females and the last cells contain males. Nests with all females or all males were found, but in no case is a female cell recorded subsequent to a male cell in the same nest.

It was interesting to find that the 2.7 average number of provisioned cells in Table I is in exact agreement with the 2.7 average given by Cooper.

Incidentally, finished nests showing only one provisioned cell were rather common in 1953, but more study is needed before this phenomenon can be associated possibly with weather conditions, availablility of prey, or parasite abundance.

Many nests were brought in from the field before the wasps had finished nesting, but rearing studies were made with the available cells. These data were combined with the records given in Table I in order to make the statistical analysis which is summarized in Table II. No significant correlation could be found between head width of reared adult wasps and length of their cells.

A decided preference was shown by the nesting wasps for holes with the 6.25 mm. diameter and 83% of the data in Table II were obtained from the burrows with that diameter. No significant differences were found between head widths of wasps reared in the different sized burrows.

Previous investigators have noted that there tends to be a definite relationship between the

sex of a wasp and the size of its cell, the female on the average developing in a larger cell than the male. Table II clearly shows that relationship in the 6.25 mm. burrow, but not in the 7.8 mm. burrow. Since the latter data are based on a limited sample, more information should be obtained before it can be concluded that the relationship of sex and cell length does not necessarily hold in burrows that are not the preferred size for the species.

It can be noted in Table II that there is a tendency toward a shorter range of cell lengths in the 7.8 mm. burrows. This may be related to a cell-volume factor, since the average volume of all cells in the 6.25 mm. burrows was 191.6 $mm.^3$, but 372.5 $mm.^3$ in the 7.8 mm. burrows.

The possible significance of the relationship of length of cell and sex of wasp was further analyzed by correlating the numbers of caterpillars used to provision cells with cell lengths as shown in Table III. Records of caterpillars in cells were usually obtained by an examination of cells before eggs of the wasp had hatched. A significant correlation was found between the length of cell and numbers of caterpillars used to provision the cell, and it can be concluded that different sized cells result from the wasp using different volumes of food to provision cells. Since on the average the larger cells contain females (as shown in the 6.25 mm. burrow in Table II) and since the egg is laid in the cell prior to provisioning, it is hypothesized that the wasp has an inherent ability to relate the amount of food provided with the sex of her egg.

Considerable variation can be expected in records associating numbers of caterpillars with cell lengths probably as a result of different species and different developmental stages of caterpillars being preyed upon by the wasp from nest to nest and season to season. For example, in a limited sample six cells averaged 8.8 ± 2.23 caterpillars and eight cells averaged 8.0 ± 2.93 caterpillars. In future studies, more exact correlations probably could be found by recording the weight of caterpillars in a cell rather than the numbers of caterpillars.

The provisions in cells were found to be caterpillars exclusively. The caterpillars were nearly immobilized and green in color when first placed in cells by the wasp, but they changed to a yellow or brown color (as plant pigments were metabolized) and became more active as the paralytic effect of the wasp sting appeared to lessen.

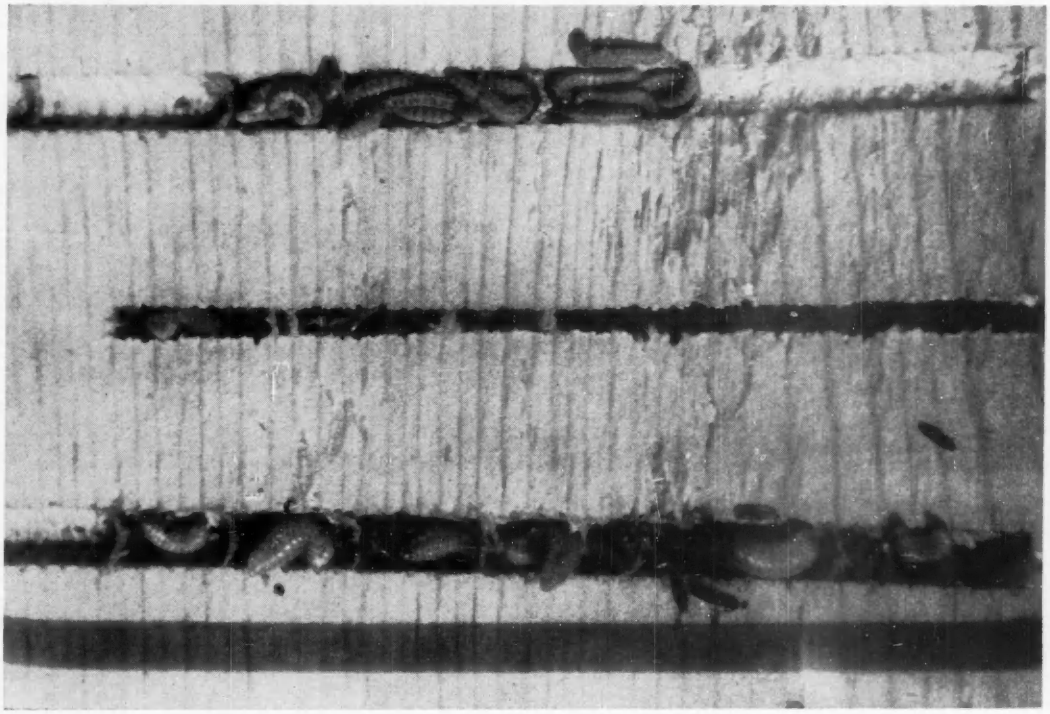

FIG. 2. A domicile trap nest opened to show details of cell construction, cell provisioning and nesting biology.

TABLE I

LENGTHS IN MILLIMETERS OF SUCCESSIVE CELLS AND SEX OF WASPS REARED IN FINISHED NESTS OF *A. antilope*. THE SEX OF WASPS IS INDICATED BY ♂ AND ♀. AN ASTERISK (*) SHOWS AN UNPROVISIONED CELL OTHER THAN THE VESTIBULAR CELL. A CELL CONTAINING A PARASITE IS SHOWN BY P, AND + INDICATES THAT THE WASP DIED BEFORE MATURITY

NEST NO.	CELL NUMBER										VESTIBULE
	1	2	3	4	5	6	7	8	9	10	
	Burrows 6.25 mm. x 150 mm.										
1	16♀	22♀	19♀	19♀	16♀	13♂					25
2	25♀	22 *	11 P	14♂	13♂	31 *					19
3	25♂	16♂	16♂	14 P	53 *						14
4	14 P	13♂	14♂	25 *	14♂	44 *					14
5	19 P	16♀	22 *								81
6	19♀	19+	14♂	63 *							28
7	6 *	16 *	16♂	16♂	75 *						13
8	11+	14♂	13+	78 *							25
9	22♀	22♀	88 *								9
10	16 *	9♂	13♂	13♂	19 P						none
11	13♀	18♀	19♀	20♀							33
12	13♂	13 *	11 P								47
13	9♂	14♂	11 P	11+	13 P	9♂	10♂	12♂	12♂	19 *	4
14	12 P	12 P	12 *	12 P	32 *	12♂	17 *	21 *			10
15	15 P	11+	12♂	11♂							6
16	13♂	11♂									39
17	14♂	12♂	13♂	11♂	10♂	12+	12♂	46 *			8
18	15♀	13 *									53
19	15♂	10 *	20 *								81
20	26♀	4 *									37
21	18♀	14 *	13♂	11 *	14 *	13♂	19 *	24 *			7
22	39 *	17♂	17♂	24 *							37
23	13♀	20 *									51
24	18♀	47 *									71
25	15♀	7 *									38
26	17♀	21 P	69 *								89
27	19♀	14♀	15♀	66 *							48
28	17♀	16♀	13♀	13♀	14♀	83 *					41
29	16♀	45 *									8
30	17♀	29 *									44
31	16♀										40
32	14 P	11♀									61
33	14♀	6 *	12 *	16♀	35 *	19 *					12
34	24♀	17 *	81 *								23
35	26 *	16♀									95
36	18 *	15 *	16+	15♀	16+						52
	Burrows 7.8 mm. x 150 mm. long										
37	( )♀	( )♀	( )♀	( )♀	( )♂	9♂	13 *				47
38	13+	10♀	12♀	16+	10 *						4
39	20♀	12♀	25 *	68 *							11
40	64 *	11♀	20 *	19 *							56
41	21♂	19 *	14 *	42 *							21
42	15♀	18 *	16♂								33
43	16♀	46 *									14
44	13♀	40 *									58

TABLE II

HEAD WIDTHS OF ADULT WASPS (0.1 MM.) AND LENGTHS OF CELLS (MM.) FROM WHICH THEY WERE REARED

SPECIMENS	HEAD WIDTH			CELL LENGTH			
	Range	Mean	Standard Deviation	Range	Mean	Standard Deviation	r
6.25 mm. burrow							
40 females	30–39	34.0	±2.21	11–31	17.6	±4.11	—0.182 n.s.
42 males	22–34	28.2	±2.37	9–25	13.5	±3.00	0.019 n.s.
7.8 mm. burrow							
12 females	31–39	35.2	±1.99	10–20	14.5	±3.34	—0.273 n.s.
5 males	25–30	27.4	±2.07	9–21	14.8	±4.38	0.616 n.s.

TABLE III

FREQUENCY OF NUMBER OF CATERPILLARS USED FOR PROVISIONS IN CELLS OF DIFFERENT LENGTHS. ALL IN BURROWS OF 6.25 MM. DIAMETER

NUMBER OF CATERPILLARS	CELL LENGTH (millimeters)						
	9	11	13	15	17	19	21
3			1				
4	2	1	4		3	1	1
5	1		2	1	1	3	
6			3				
7			6			1	
8			2			1	2
9			2		1	3	
10					1	1	
11				1			
12						1	
13					1		

Correlation (r) = 0.305*

TABLE IV

REPRESENTATIVE TIMETABLE OF THE OVERWINTERING GENERATION OF *A. antilope*

DEVELOPMENTAL STAGE	SPECIMEN NUMBER			
	1	2	3	4
Egg		Aug. 23	Sept. 7	
Small larva	Sept. 7			
Full grown larva	Sept. 12	Aug. 31	Sept. 14	July 17
Cocoon started	Sept. 16			
Cocoon complete		Sept. 8	Sept. 22	
Larvae form in cocoon	April 10		April 10	
White pupal form	May 18		May 13	
Pupa started coloration		May 26	May 26	May 26
Pupa completed coloration	June 3			June 3
Adult emerged	June 14	June 14	June 16	June 16

A rather wide range of host species is used for provisions in Wisconsin. Nests were found to include the following caterpillars[2]:

EPIPASCHIIDAE
Tetralopha sp.
GELECHIIDAE
Doubtfully *Anacampsis* sp.
Genus & sp.?
PHALAENIDAE
Genus & sp.?
PHYCITIDAE
Mineola indigenella (Zell.)
Salebria subcaesiella (Clem.)
Nephopteryx sp.
Genus & Sp.?
TORTRICIDAE
Archips cerasivorana (Fitch)
Archips fervidana (Clem.)
Archips sp.
Genus & sp.?

The trap-nest technique also enabled us to study the life cycle of the wasp. A summer generation was started during late June and early July. The female wasp suspended an egg from the top of the cell by means of a slender thread, and then proceeded to provision the cell. Table I shows the diversity of nest construction. It is to be expected that the length of time required to complete a nest varies with the season, the weather and the number of provisioned cells.

The developmental stages averaged as follows: the larval stage was completed at 7.3 days, cocooning occupied 1.3 days and the pupal stage was ended at 18.8 days. Therefore the average life cycle from the time of hatching of the egg to emergence of the adult was 27.4 days. The timetable of the developmental stages was found to be comparable with data given by Cooper. In a few cases not included in the above averages, a pupa lagged in development and that stage occupied 32.3 days. These individuals were from nests made in late June, hence the extended pupal period may have been the result of the rearing method, rather than the broken diapause of a form destined for overwintering.

Data representative of the overwintering generation are given in Table IV. Most of these nests were started in late August and early September. The full grown larvae passed the winter encased in a cocoon and pupated in the spring. Adults emerged in the middle of June. In nature, these individuals would give rise to the summer generation. An individual of the summer generation entering diapause is shown by the data given for specimen 4. This record is in agreement with observations discussed by Cooper.

At least 25 percent of the wasps developing in the provisioned cells were fated for death before emerging as adults. The major mortality factors were insect parasites and pathogens. Indirectly, the spoilage of provisions also may have caused starvation of larvae, especially when reared in vials. Additional records of the insect parasites are being obtained, and it is proposed to report upon this research in a subsequent paper.

[2]Grateful acknowledgement is made to H. W. Capps, U. S. National Museum, for the determinations of caterpillars. The caterpillars collected by Cooper also were identified by H. W. Capps. Four different kinds were recognized, these being pyralids and presumably gelechiids, with the latter forming about 80% of the prey.

LITERATURE CITED

Cooper, K. W. 1953. The ecology, predation and competition of *Ancistrocerus antilope* (Panzer). Trans. Amer. Ent. Soc. 79: 13–35.

THE NATURAL CLASSIFICATION OF THE FAMILIES OF COLEOPTERA, by ROY A. CROWSON. Pp. 187, 213 figs. Nathaniel Lloyd & Co., Ltd., (Burwell Str. Works, Blackfriars) London. 1955. 30s. in paper covers; in full cloth 6s. extra; postage 6d. extra.

This book is essentially a reprint of a series of articles published in 16 numbers of *The Entomologists Monthly Magazine* between May 1950, and March 1954. To these, however, have been added the characterization of a new, fourth, suborder of Coleoptera, a tabulated synopsis of the system proposed, and an alphabetical index of about 1300 names of genera and higher groups. The author, who is Lecturer in Zoology at the University of Glasgow, humbly dedicates, as he says, his small work in the same field to the memory of Prof. T. Lacordaire, Tome I of whose great work "Genera des Coléoptères" appeared in 1854. And it is a book that should be present in every library the owners or directors of which profess more than the merest amateur interest in beetles.

By means of keys and brief discursive text the classification is carried to the level of subfamilies. The beetles are divided into 4 suborders; 22 superfamilies (including the Stylopoidea); and 191 families. The keys are not intended for ordinary determination work, but as a convenient method of setting out the theoretical basis of the classification. The author hopes, however, that use will be made of the keys by persons confronted with unknown species of doubtful family attribution.

An important feature of the book is that, wherever such information is available, distinguishing larval characteristics are cited in the keys immediately following the characters of the adult.

As previously intimated, this is a book to which every serious coleopterist should give close and repeated study. While it undoubtedly does not represent the final word on the natural classification of the Coleoptera—that word will not be written until men have lost interest in the problems represented—it is a document that will be referred to by Mr. Crowson's successors in this difficult field for many years.

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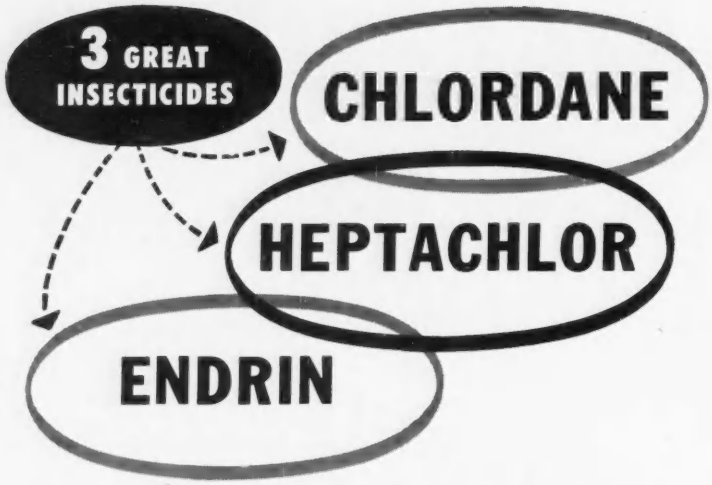

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